

FOSSIL LAND SNAIL FAUNAS OF PORTO SANTO, MADEIRAN ARCHIPELAGO: CHANGE AND STASIS IN PLEISTOCENE TO RECENT TIMES

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ABSTRACT

Samples of fossil land snails were made at 14 sites on the island of Porto Santo, Madeiran archipelago. Material in stratigraphical sequences could be dated by A/I racemization calibrated against radiocarbon dating, and against Uranium/Thorium estimates based on Madeiran material. Although errors associated with the oldest samples are large, it is clear that the oldest shell-bearing deposits are at least 300 ka old, and probably much older. Some taxonomic difficulties have been resolved by morphometric studies. The geographical pattern in the fossils (in both faunal composition and morphometrics) resembles closely that seen today, the southwest of the island being particularly distinctive. Of 58 native taxa found in the deposits, 22 are extinct on the island, though four still survive on Madeira. Extinction has been greater in the southwest than elsewhere, and early fossil faunas there are richer than later ones. As on Madeira, more than half of this extinction seems likely to be the consequence of human disturbance, which has also reduced and fragmented the ranges of other species. The overall pattern is of distributional stasis in many species, reduction of range or extinction in many others, but very few cases of range expansion. Neither extinctions nor changes in apparent abundance can be related to known changes in global climate over the period involved. This relative stasis is in marked contrast to the situation on Madeira, only 40 km away, where there are temporal shifts in the fauna, and evidence of colonization events. Possible reasons for this difference are discussed.

Key words: Fossil land snails, Porto Santo, Pleistocene, Holocene.

INTRODUCTION

The Madeiran archipelago has a rich land snail fauna, with many endemic species and high levels of differentiation between habitats and islands. This diversity has been studied since the 19th century (Lowe, 1831, 1852, 1854; Albers, 1854; see Wilson, 1970). Some of the features have been reviewed, along with new data, by Waldén (1983, 1984), by Cameron & Cook (2001) for Madeira, Cameron et al. (1996b) and Seddon (1995) for Porto Santo, and Cameron & Cook (1999) for the Deserta islands. In addition to information on modern distribution and species associations, there are records from fossil deposits on the history of the fauna, making the islands an

exceptional centre for study of an evolutionary radiation. We have examined dated fossil material from the eastern peninsula of Madeira (Cook et al., 1993; Goodfriend, 1994, 1996) and from the Desertas (Cameron & Cook, 1999).

The fossil faunas of Porto Santo have received less attention. Wollaston (1878) reviewed early work, and there have been some later taxonomic and individual site reports. This paper gives results of extensive sampling on Porto Santo and its adjacent islets by Goodfriend, Cameron and Cook, and, independently, by Seddon. Both series are accompanied by stratigraphical notes, but only the former was subject to dating analysis, carried out by Goodfriend, and incomplete at the time of his death. The extent of shell-bearing de-

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*Authorship of this paper is in alphabetical order. The collections were made by Goodfriend, aided by Cameron and Cook, and at different times and places, by Seddon. The dating is entirely the work of Glenn Goodfriend, who died in 2002; had he survived he would have been senior author. As it is, the paper is dedicated to him in memory of his companionship and pioneering work on geochronology.

posits on the island is vast (at least half the present surface area is covered by aeolian or colluvial deposits) and the stratigraphy is complex. Sampling sites were spread broadly across the island, providing an opportunity to look not only at species associations and possible temporal changes but also at micro-geographical variation. There are marked differences in the present fauna from one part of the island to another (Cameron et al., 1996b) and some interesting evolutionary patterns.

METHODS

Goodfriend's Samples

(a) *Stratigraphy and Dating.* Locations were sought where exposed sequences of aeolian sands or colluvial deposits could be examined for molluscan shells (Fig. 1). Stratigraphical notes were made in the field. Snail shell samples (and in a few cases bird egg shell)

that were definitely *in situ* were collected for dating. Chronology is based on measurements of D-alloisoleucine: L-isoleucine (A/I) ratio (Goodfriend, 1987) using gas chromatography (GC) and high performance liquid chromatography (HPLC), calibrated against radiocarbon dating. The snail species tested were *Caseolus bowdichianus*, *C. punctulatus*, *Helix subplicatus*, *Leptaxis chrysomela*, and *Theba pisana*, chosen because their shells are relatively robust and they cover a wide range of possible dates. *Theba pisana* is a non-endemic that arrived recently, whereas the others are endemic to the islands.

(b) *Site Choice and Methods.* Goodfriend took samples at 13 sites in 1990 and 1993, and an additional site (No. 11) was sampled by Cook in 1993 (Fig. 1). At five sites (1, 2, 6, 7 and 12/10), several samples were taken to cover the apparent stratigraphical range. At Fonte de Areia (Sites 1 and S3), the exposed sections were approximately 1 km long and up to 40 m

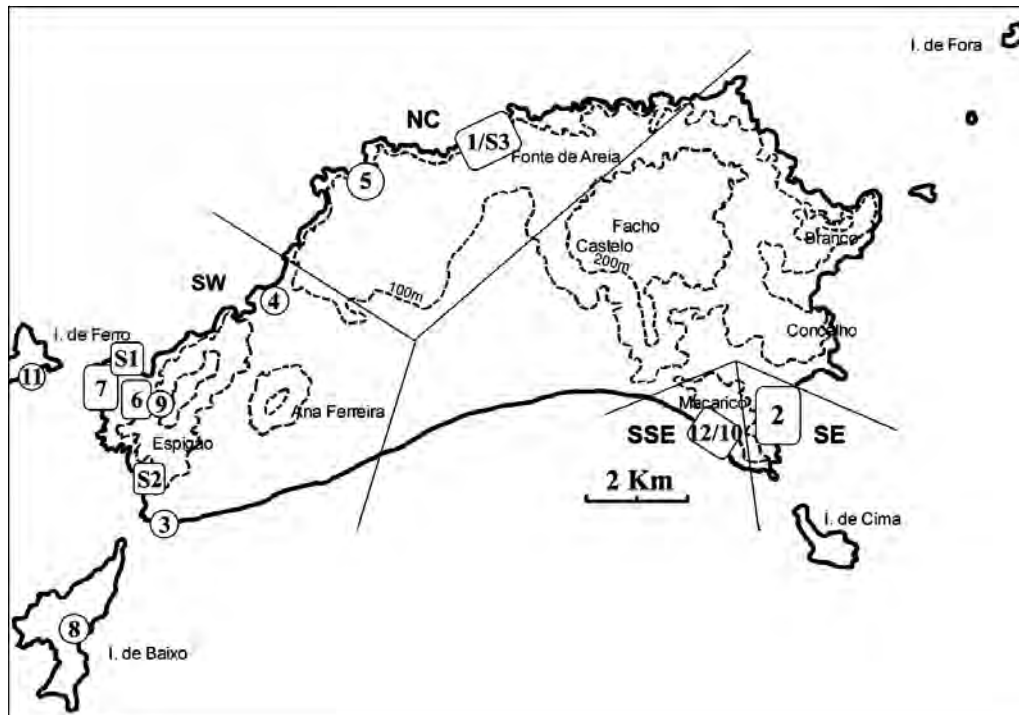


FIG. 1. Map of Porto Santo and islets showing collecting sites. Site 13 is within the area of site 10/12. Circles: sites with only one or two samples only; squares: sites with three or more samples. Site numbers prefixed by 'S' are Seddon's sites. Regions: SW: southwest, NC: north-central, SE: southeast, SSE: south-southeast.

in height, and although sampling was not possible from a single vertical column, the stratigraphical position of each sample could be reliably determined. The nature of the terrain elsewhere was often such that collecting had to be distributed amongst several exposures. At most, these were separated by 500 m; generally, the distance was less than 100 m. Sites 10 and 12 were adjacent and have been combined as a single site. Relative stratigraphical positions could be determined by a combination of the character of strata, topography and A/I values. Other sites were sampled in a more exploratory way, looking at one or two strata only. Shells of terrestrial snails were collected (see below) at all but Site 13, within the area of 12/10, from which fossil limpet shells were removed for A/I analysis to provide a basal date for sediments sampled in Sites 10 and 12. At some sites with few shells material was collected solely for A/I analysis.

Shells were collected from cleaned and vertically defined sections of the profile, and character and depth of exposed sediments were recorded. In many cases, the matrix was indurated and shells were dug out singly. Sometimes it was possible to sieve a section of the profile through meshes down to 0.5 mm. Since extraction techniques varied, our analyses generally concern presence and absence data, but the numbers of shells of each species found are shown in the appendices and are discussed in particular contexts.

(c) *Sites*. Goodfriend made stratigraphical, topographical and location notes for each site and sample. From these, and from the results of A/I analyses, we have ordered samples by age, using the stratigraphy to place those lacking A/I determinations. Cases where stratigraphical position and A/I ratios give contradictory results are explained in the appendix. Site descriptions are provided in Appendix 1. The locations with most complete samples are Sites 1, 2, 6, 7, 12/10, S1, S2, and S3, and some analyses use only these series.

Seddon's Samples

Seddon's samples were taken at 13 sites, usually from cleaned and vertically defined sections. Most were of fixed substrate weight, and the shells were extracted by sieving down to 0.5 mm mesh. Many were post-human colonisation deposits, containing the intro-

duced *Theba pisana*. Here we consider only three sites with older strata, where the stratigraphical context of each sample was clear. Locations of Seddon's samples are shown in Fig. 1, with details in Appendix 1.

IDENTIFICATION AND NOMENCLATURE

Most of the taxa known from fossil deposits on Porto Santo were described in the nineteenth century, and discussed by Wollaston (1878). The fauna of the archipelago as a whole was revised by Waldén (1983), including all taxa known only from fossil shells, and incorporating work done subsequent to Wollaston's monograph. Waldén visited many museums, comparing types with other material in the museums, and with his own collections. In the Natural History Museum, London, in the National Museum of Wales, Cardiff, and in the Manchester Museum, he inserted labels giving his diagnoses of lots. We have compared our material with his diagnoses.

Waldén (1983) used trinomials (nominal subspecies) for forms with distinctive features that did not, in his view, merit species status. It is not always clear whether these forms have separate geographical or temporal ranges. Many were regarded as varieties by Wollaston (1878), whose material was usually not localised within islands.

Of necessity, fossil taxa are defined on conchological characters, despite their known unreliability in living taxa. Erosion of surface features can make determination difficult, especially in the genus *Caseolus*.

Since Waldén's (1983) account, some new taxa have been described, the nomenclature reassessed and a new provisional checklist published (Bank et al., 2002). Seddon (in press) will provide an up-to-date synonymy, and papers describing new taxa are included in the references. We have followed the names and sequence in Waldén (1983), with some exceptions, additions and qualifications. We have refrained from introducing new names, but use a few synonymies and aggregate taxa where characters are hard to determine. A wider spread of samples often blurs the distinction between taxa described from single samples in which apparently distinctive forms were found. Goodfriend's material was identified by RADC, and Seddon's material by her. Subsequently, the two sets were compared for consistency. Exceptions are:

- *Leiostyla subcorneocostata* Seddon, 1990. A close relative of the extant *L. corneocostata* (Wollaston, 1878).
- *Leiostyla espigaoensis* Seddon, 1990.
- *Phenacolimax portosanctanus* Groh & Hemmen, 1986a.
- *Phenacolimax crassus* Groh & Hemmen, 1986a.
- *Eucobresia media* (Lowe, 1854). Omitted by Waldén (1983) but reinstated by Groh & Hemmen (1986a).
- *Heterostoma pauperula* (Lowe, 1831). Includes all forms referred by Waldén (1983) to *Heterostoma* or *Steenbergia*. A morphometric analysis is given below.
- *Geomitra acarinata* Hemmen & Groh, 1985.
- *Geomitra gerberi* Groh & Hemmen, 1986b.
- *Spirobula latinea* (Paiva, 1866). This name is not used, based on morphometric evidence (see below) that it is an extreme form of *S. depauperata* (Lowe, 1831).
- *Caseolus compactus* (Lowe, 1831). Forms described under this name undoubtedly belong to more than one species. Waldén (1983) listed two extant, and three extinct subspecies, relating some to varieties described by Wollaston (1878). The diagnostic characters often involve shell sculpture characters, which are frequently abraded in fossil shells, and, sometimes seem to show continuous variation. We have generally distinguished between large and small shells, as the distinction is often marked, with no evident intermediates. In the best-preserved material, it is sometimes possible to assign shells to the designated subspecies *C. c. ariensis* Waldén, 1983, and *C. c. vigiae* Waldén, 1983. In the latter case, comparison with identified material in museums suggests that there may be confusion with *C. baixoensis* Waldén, 1983, a species allied to *C. commixtus* (Lowe, 1854) (see below). We have not recognised the latter in our samples.
- *Caseolus consors* (Lowe, 1831). In general, this is a well-characterised species, but in older deposits it sometimes resembles large forms of *C. compactus*.
- *Caseolus abjectus* (Lowe, 1831). In the modern fauna, this species has a close relative, *Caseolus commixtus* (Lowe, 1854), which is usually clearly distinguishable. In subfossil samples, the distinction is hard to make: the taxon *C. abjectus* agg. includes forms that could be placed in *C. commixtus*.
- *Caseolus subcalliferus subcalliferus* (Reeve, 1854), and *C. s. submajor* Waldén, 1983. The latter is very abundant in some Pleistocene/Holocene deposits, but appears to be extinct. The two forms are occasionally found together. We have treated them as species, but have retained Waldén's nomenclature.
- *Caseolus punctulatus* (G. B. Sowerby I, 1824). We include specimens that might be assigned to *C. solidus* (Lowe, 1831). Both species are deemed to be extant, but modern populations show continuous variation in diagnostic characters.
- *Discula bicarinata* (G. B. Sowerby I, 1824). Appears to be distinct at species level from *D. b. aucta* (Wollaston, 1878). We have retained Waldén's nomenclature.
- *Discula oxytropis* (Lowe, 1831). Waldén listed two extinct subspecies, *D. o. subcarinulata* (Wollaston, 1878), and *D. o. vermetiformis* (Lowe, 1854). These taxa are problematic. We present morphometric data below, and treat all our material as *D. oxytropis*.
- *Discula calcigena* (Lowe, 1831), *D. pulvinata* (Lowe, 1831), and *D. attrita* (Lowe, 1831). We have retained these names, despite difficulties with some specimens. Waldén (1983) listed five subspecies of *D. calcigena*, one of which, *D. calcigena discina* is regarded by some as a species. We have not used these subspecific distinctions. In the deposits, and in modern faunas (Cameron et al., 1996b), we find pairs of the three species level taxa present syntopically with no intermediates.
- *Discula albersi* (Lowe, 1852). Regarded as a synonym of *D. bulweri* (Wood, 1828).
- *Leptaxis* sp. In two sites, we have specimens of a form similar to *L. erubescens* (Lowe, 1831) or *L. furva* (Lowe, 1831) but not matching either exactly. *L. furva* is a montane species, known only on Madeira (Wollaston, 1878). *Leptaxis erubescens* occurs in the modern Porto Santan fauna only on the upper slopes of the highest hill, Pico do Facho.
- *Leptaxis* cf. *fluctuosa*. Waldén (1983) regarded this form as a subspecies of *L. chrysomela* (Pfeiffer, 1848). While it is very variable, we regard it as a species-level taxon.
- *Leptaxis granulosa*, Groh, 1983. Known only subfossil (Groh, 1983) and here regarded as a synonym of the also extinct *L. psammophora*.

All species in our samples, with the exception of *Theba pisana* (Müller, 1774), *Punctum pygmaeum* (Draparnaud, 1805), and *Plagiorona placida* (Shuttleworth, 1852), are endemic to the Madeiran archipelago, but *Heterostoma paupercula* and *Leptaxis erubescens*, the latter not recorded in our samples but extant on Porto Santo, have been introduced in the Azores (Backhuys, 1975).

RESULTS

Chronology

A total of 220 A/I racemization determinations was made on material from 51 stratigraphical sections at 12 locations. About three quarters were HPLC measurements and the rest GC; there is good agreement between the two. Excluding three measurements that obviously refer to redeposited shells (in samples 2-6, 2-10 and 7-1) and a section for which there is a single measurement, the variation between sections is highly significant ($F = 47.3$, $50/165$ d.f.). The within-section standard error is 0.0056. The measurements therefore show consistency within sections and allow clear distinctions to be made between them.

Correction and calibration of the A/I data for Porto Santo is incomplete, but at selected levels in the younger parts of sequences radiocarbon analysis of shell carbonate has provided points corresponding approximately

to known ages. There are four samples available, ranging from 0.140, corresponding to an age of 3.7 ka, to 0.381, corresponding to > 47 ka. These figures fit well with the 17 records for Madeira (Goodfriend et al., 1996; Cameron & Cook, 1999), which include two Uranium/Thorium dates for older samples. Techniques and qualifications relating to the Madeiran deposits were discussed by Goodfriend et al. (1996). The pooled data from reliable pre-colonisation determinations for both islands provide a good linear relation of log years on ratio ($\log_{10} \text{years} = 10.4822 \text{ A/I} + 7.2432$, $r^2 = 0.929$). This does not represent the relationship for very recent times (see discussion in Goodfriend et al., 1996), but for intermediate values a ratio of 0.2 corresponds to an age of about 11 ka and 0.4 to about 93 ka. At the limit of available calibration, an A/I ratio of 0.5 corresponds to about 263 ka. At the largest mean A/I ratios (around 0.8) small errors have large effects; the logarithmic equation above gives an estimate of approximately 6 Ma. This is unlikely to be correct, on stratigraphical grounds at least, but the oldest samples may be more than one million years old.

Mean A/I ratios for the 5 GAG sites subject to detailed faunal analysis are shown in Figure 2. Sites 2, 6, and 12 contain no horizons as old as those in Sites 1 and 7. Samples from the base of the uppermost stratigraphical unit of Site 1 (1-1) provide 4 A/I ratios with a range from 0.308 to 0.422 (mean 0.349), and a radiocarbon age of > 47 ka. This is beyond the

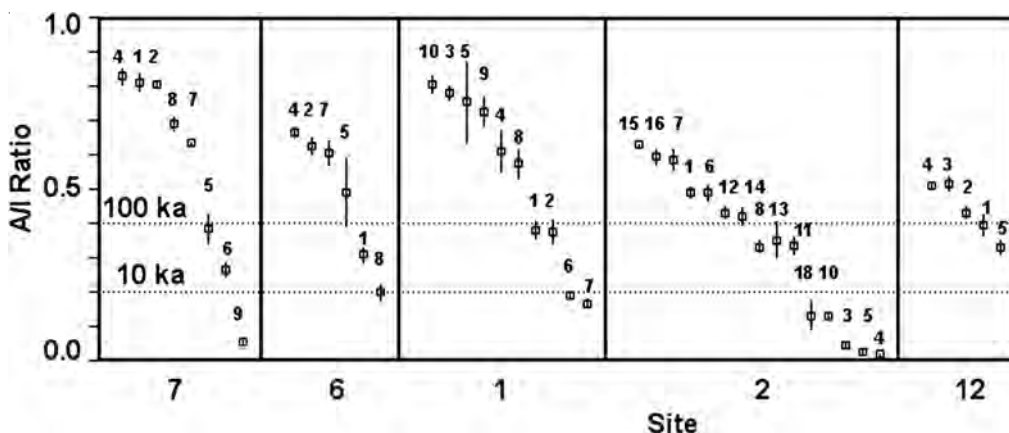


FIG. 2. D-alloisoleucine:L-isoleucine (A/I) values for sampled sections at faunal analysis sites arranged in descending order of age. Means and standard errors are given for readings from each section, and section reference numbers are shown. Dotted lines indicate ages of approximately 10 ka and 100 ka based on calibration by radiocarbon dating.

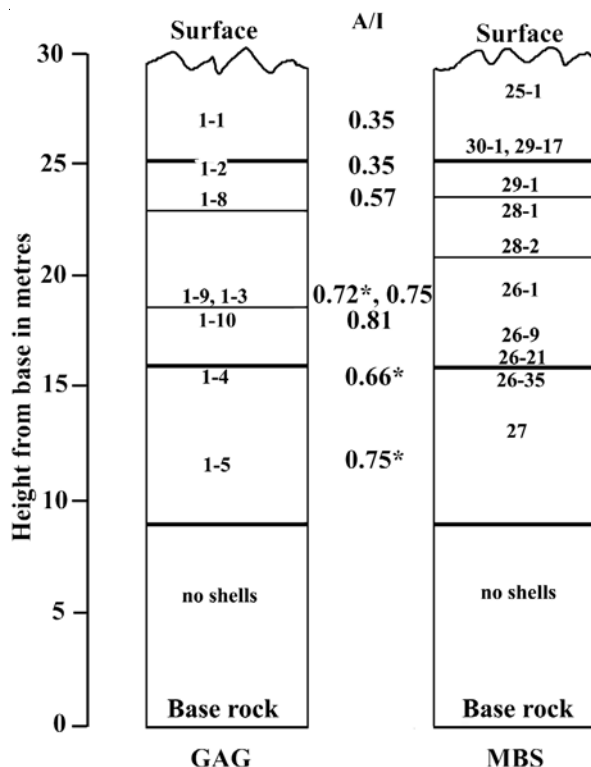


FIG. 3. Diagrammatic stratigraphical section at Fonte da Areia, showing the relative positions of samples from Sites 1 and S3. The sample sequences are shown relative to the base rock underlying the sediments. Thick horizontal lines represent strata boundaries that can be aligned between the two sequences with a high degree of confidence; the thinner lines represent discontinuities in each, which may not be equivalent (see Appendix 1). Mean A/I ratios are shown for Site 1 samples; asterisked values indicate variability in results for individual shells. Note that Site 1 samples do not come from a single column, and the depths of strata vary from place to place in the exposure.

limit of reliable determination, but considerably older than the 21 ka suggested by Lietz & Schwarzbach (1971) for the same horizon.

Fig. 3 compares and aligns samples from Site 1 and Site S3, which come from the same stratigraphical sequence on the north coast, and relates them to the range of A/I values (Appendix 1). Samples 1-6 and 1-7 (Holocene) were made away from the main stratigraphical sequence, and are excluded. Sample S3-27 matches 1-5 in the abundance and composition of its material (Appendices 4 and 7). With the exception of 1-4, all samples less than 20 m from the base have A/I ratios > 0.7, and those between 20 and 24 metres have A/I ra-

tios in the range 0.4–0.7. We are unable to assign the neighboring samples S1 and S2 to any of these bands. S1 has a relatively poor fauna resembling that of Site 6. S2, however, is the most distinctive in the whole array, with seven species unique to it (Appendix 8), of which six are extinct. These deposits are probably old, and their colluvial nature may have resulted in faunal mixing.

Faunal Composition

The faunal composition of successive layers for Sites 7, 6, 1, 2, 12/10, S1, S2 and S3 (sites with more than two samples) is given in

Appendices 2–8. Appendix 9 gives the results for the remaining sites. Overall, 59 taxa were recognised, 22 of which are extinct (37.3%). Given the uncertainties and aggregate categories referred to above, this is a minimum number. The following list 1 shows the status of these taxa, along with that of other taxa recorded on Porto Santo, but not present in these samples (Seddon, in press).

Present, extinct, endemic:

Craspedopoma mucronatum
Truncatellina linearis
Staurodon saxicola
Leiostyla subcorneocostata
Leiostyla espigaoensis
Phenacolimax crassus
Phenacolimax portosanctanus
Geomitra acarinata
Caseolus cf. compactus vigiae
Caseolus subcalliferus submajor
Caseolus bowdichianus
Actinella arcinella papillosa
Actinella crassiuscula
Actinella morenensis
Discula bicarinata aucta.
Discula cockerelli
Pseudocampylaea lowei
Leptaxis sp.
Leptaxis chrysomela
Leptaxis cf. fluctuosa

Present, extinct, non-endemic:

Punctum pygmaeum
Plagyrona placida

Absent, extinct, endemic:

Geomitra gerberi
Discula echinoderma
Leptaxis psammophora

Present, extant, endemic:

Leiostyla calathiscus
Leiostyla monticola
Amphorella melampoides
Amphorella triticea
Amphorella oryza
Amphorella gracilis
Amphorella cf. cimensis
Cyllichnidia ovuliformis
Boettgeria lowei
Heterostoma paupercula
Geomitra coronata
Spirorbula obtecta
Spirorbula depauperata
*Caseolus compactus (large)**

*Caseolus compactus (small)**
Caseolus consors
Caseolus abjectus agg.
Caseolus subcalliferus subcalliferus.
Caseolus hartungi
Caseolus calculus
Caseolus punctulatus
Actinella effugiens
Discula rotula
Discula bicarinata
Discula oxytropis
Discula cheiranticola
Discula calcigena
Discula pulvinata
Discula attrita
Discula bulweri
Discula tectiformis
Pseudocampylaea portosanctana
Leptaxis nivosa
Leptaxis wollastoni
Lampadia webbiana
Helix subplicata

Present, extant, non-endemic:

Theba pisana

Absent, extant, endemic, not fossil:

Leiostyla corneocostata
Leiostyla relevata
Leiostyla ferraria
Amphorella tuberculata
Amphorella terebella
Eucobresia media
Lemniscia michaudi
Discula echinulata
Discula turricula
Leptaxis erubescens

Absent, extant, endemic, fossil:

Cecilioides eulima
Discula leacockiana
Discula testudinalis

Absent, extant, non-endemic:

Vitrea contracta
Oxychilus alliarius
Cecilioides acicula
Rumina decollata
Balea perversa
Cochlicella acuta
Cochlicella barbara
Caracollina lenticula

*Some forms of *C. compactus*, for example *C. compactus areiensis*, appear to be extinct. Slugs, all non-endemic, are excluded.

Table 1. Species unique to samples at Site 1 and S3, at Fonte da Areia. Asterisked species were found only in late Holocene deposits not sampled at S3 (1-6 and 1-7).

Species Site 1 only	Nos.	Species Site S3 only	Nos.
<i>Amphorella oryzae</i>	5	<i>Staurodon saxicola</i>	2
<i>Caseolus consors</i>	3*	<i>Leiostyla subcorneocostata</i>	1
<i>Actinella crassiuscula</i>	21	<i>Leiostyla calathiscus</i>	8
<i>Discula cheiranticola</i>	1*	<i>Phenacolimax portosanctanus</i>	27
<i>Pseudocampylaea portosanctana</i>	20	<i>Caseolus calculus</i>	18
<i>Pseudocampylaea lowei</i>	4	<i>Discula bicarinata aucta</i>	3
		<i>Discula calcigena</i>	2
		<i>Discula pulvinata</i>	1
Total shells recovered	2121	Total shells recovered	1830

Among endemics, only three extinct species recorded for the island were absent from our samples. Of the 13 extant endemic species not found, only three have previously been found subfossil; most of the rest are restricted to rocky hills, or have otherwise limited distributions away from our sites. Only three non-endemic species were recorded in our samples. Two of them, *Punctum pygmaeum* and *Plagyrona placida* are recorded here for the first time on Porto Santo; they are unknown in the modern fauna. As on Madeira (Goodfriend et al., 1996), their presence predates human colonisation, and like the locally extinct endemics *Craspedopoma mucronatum* and *Staurodon saxicola*, they both survive on Madeira. *Theba pisana*, by contrast, is common and widespread. Its arrival is thought to follow human occupation of the island in the early 15th century AD.

Inspection of the appendices shows that the number of taxa recorded at each site is related to the number of samples made, which reflects both total number of specimens collected and the time spent collecting. Individual samples also vary in the number of taxa found, which is correlated with the total number of shells in each sample. Absences may therefore be caused by inadequate sampling, especially in individual samples. Even at site level, there are differences. For instance, the faunal composition of Sites 1 and S3, which represent the same stratigraphical sequence, are very close to each other, and have large numbers (Table 1). Two species found only at Site 1 were recorded only in Holocene deposits (1-6 and 1-7) not sampled at Site S3, where fossil *P. portosanctana* and *P. lowei* were loose on the surface. The larger number of species found at Site S3 show both that very rare species may be missed by accident, and that the

smallest species may be missed when a sample is obtained by hand collecting from the substrate (Site 1) rather than sieving (Site S3).

Geographical Pattern

The modern distribution of snails on Porto Santo shows geographical differentiation (Cameron et al., 1996b). Site results have therefore been amalgamated on a regional basis (Fig. 1) to reflect this, and also to reduce the effect of sampling error (Table 2). Note that the inclusion of many sites with one or two samples in the SW region does not have much influence on the overall fauna recorded. The two offshore island samples included here (8 and 11) contain no species not found elsewhere. While the aggregate fossil faunas of all regions are similar, the Nei indices of similarity (Table 3) show SW and NC to be most similar, followed by the SE and SSE regions. 19 species are found in all four regions, and a further 16 are found in both the aggregated regions. Table 4 shows the remaining species with restricted, but coherent distributions. The SW region has many more unique species than the remainder, and the SW and NC regions combined have more than the SE and SSE combined. There is, however, a big difference in the character of the unique species; in the SW/NC area, 10 of the 15 are extinct, whereas only one out of eight is extinct in the SE/SSE area. In our samples seven species are unique to site S2 (SW region); six of these are extinct: the non-endemics *Punctum pygmaeum* and *Plagyrona placida*, the endemics *Leiostyla espigaoensis* and *Actinella morenensis* for which this is the type and only known locality (Seddon, 1990), and the endemics *Phenacolimax crassus* and *Geomitra acarinata*, known from earlier work.

Table 2. The occurrence of fossil taxa in each region of Porto Santo. Note that *Theba pisana* was present in all four regions, but is excluded from formal analyses, as it appears to be an introduced species.

Species/Sites	SW	NC	SE	SSE
<i>Craspedopoma mucronatum</i>	1	1		
<i>Truncatellina linearis</i>	1	1		1
<i>Staurodon saxicola</i>	1	1		1
<i>Leiostyla subcorneocostata</i>	1	1		
<i>Leiostyla espigaoensis</i>	1			
<i>Leiostyla calathiscus</i>		1		1
<i>Leiostyla monticola</i>		1	1	1
<i>Punctum pygmaeum</i>	1			
<i>Plagyrona placida</i>	1			
<i>Phenacolimax crassus</i>	1			
<i>Phenacolimax portosanctanus</i>	1	1	1	
<i>Amphorella melampoides</i>	1		1	1
<i>Amphorella triticea</i>	1	1	1	1
<i>Amphorella oryza</i>	1	1	1	1
<i>Amphorella gracilis</i>			1	
<i>Amphorella cf. cimensis</i>	1			
<i>Cylichnidia ovuliformis</i>	1		1	1
<i>Boettgeria lowei</i>	1		1	1
<i>Heterostoma paupercula</i>	1	1	1	1
<i>Geomitra coronata</i>	1	1	1	1
<i>Geomitra acarinata</i>	1			
<i>Spirorbula oblecta</i>				
<i>Spirorbula depauperata</i>	1	1	1	1
<i>Caseolus compactus</i> (large)	1	1		
<i>Caseolus compactus</i> (small)	1	1	1	1
<i>Caseolus cf. compactus vigiae</i>	1	1	1	1
<i>Caseolus consors</i>	1	1	1	1
<i>Caseolus abjectus</i> agg.	1	1	1	1
<i>Caseolus subcalliferus submajor</i>	1	1	1	
<i>Caseolus subcalliferus subcalliferus</i>	1	1	1	1
<i>Caseolus hartungi</i>	1			
<i>Caseolus calculus</i>		1		
<i>Caseolus punctulatus</i>	1	1	1	1
<i>Caseolus bowdichianus</i>	1	1	1	1
<i>Actinella arcinella</i> pap.	1	1	1	1
<i>Actinella crassiuscula</i>	1	1		
<i>Actinella effugiens</i>	1		1	1
<i>Actinella morenensis</i>	1			
<i>Discula rotula</i>			1	
<i>Discula bicarinata</i>			1	
<i>Discula bicarinata aucta</i>	1	1	1	
<i>Discula oxytropis</i>			1	1
<i>Discula cheiranticola</i>	1	1	1	
<i>Discula calcigena</i>	1	1		1
<i>Discula pulvinata</i>	1	1	1	
<i>Discula attrita</i>	1	1		
<i>Discula bulwerii</i>				1
<i>Discula cockerelli</i>				1
<i>Discula tectiformis</i>	1	1	1	1

(continues)

(continued)

Species/Sites	SW	NC	SE	SSE
<i>Pseudocampylaea portosantana</i>	1	1	1	1
<i>Pseudocampylaea lowei</i>	1	1	1	1
<i>Leptaxis</i> sp.	1			
<i>Leptaxis chrysomela</i>		1	1	
<i>Leptaxis</i> cf. <i>fluctuosa</i>	1	1	1	1
<i>Leptaxis nivosa</i>	1	1	1	1
<i>Leptaxis wollastoni</i>			1	1
<i>Lampadia webbiana</i>			1	
<i>Helix subplicata</i>	1	1		1
<i>Caseolus hartungi</i>	1			
<i>Caseolus calculus</i>		1		
<i>Caseolus punctulatus</i>	1	1	1	1
<i>Caseolus bowdichianus</i>	1	1	1	1
Total No. of taxa	46	37	36	33
Total No. of samples	31	23	16	6

Changes with Time: the Fauna Overall

Using the A/I data, relating undated to dated samples stratigraphically, and using the presence of *Theba pisana* as an indicator of very recent age, we can allocate samples to age categories. Two dividing lines have been used: at A/I value of 0.2, separating all but the earliest Holocene from older deposits, and at A/I = 0.4, separating the last cold phase of the Pleistocene from earlier periods including warm interglacials with high sea levels. For some analyses, we use a further division at A/I = 0.7, to study the contribution of the oldest faunas at Sites 1, S3 and 7 to temporal and geographic patterns. Table 5 shows species by their temporal ranges within the deposits. Excluding the introduced *T. pisana*, there are 58 taxa in the array. 55 of these are found in the earliest division (A/I > 0.4), assuming that material from S2 is assigned to it, 43 between A/I 0.2 and 0.4, and 31 from Holocene deposits (A/I < 0.2). There is thus a decline in observed richness with time. The occurrence of

extant species in either or both of the two earlier divisions, but not in the Holocene, however, tells us that the examined fossil record is incomplete. Conversely, two species are restricted to Holocene deposits, and one is found only in the A/I range 0.2–0.4. All three are extant, small and rare as fossils. One other extant species, *Caseolus hartungi*, is present before A/I 0.4 and after A/I 0.2 but not between. It was found in small numbers in only two samples. 29 species, 50% of the total, occur in all three divisions, including the most abundant species in each. Eight of these are, however, extinct.

Assuming samples from S1 and S2 are at least A/I > 0.4, we can conclude that at A/I > 0.4, 22 are extinct (40%); at A/I 0.2–0.4, 11 are extinct (25.6%), and at A/I < 0.2, 8 are extinct (25.8%). Given the great disparity in times covered by each division it is apparent that extinction rate within the Holocene is far greater than in earlier periods. We note that if S1 and especially S2 represent younger deposits, the rates of extinction in later divisions would be even higher.

In the earliest deposits (A/I > 0.7, only present in the SW and NC regions: Sites 1, S3, and 7) 32 species are recorded, of which 11 (34.4%) are extinct. Fifteen species recorded at A/I > 0.4 (inclusive of these early samples, but excluding S2) are thus missing, but six of these are not known at all from the SW or NC regions, either fossil or modern. Samples within A/I 0.4–0.7 are found in all regions; if we remove the samples (A/I > 0.7),

Table 3. Values of the Nei index of faunal similarity in between region comparisons.

	NC	SE	SSE
SW	80.0	68.5	68.3
NC		71.2	70.5
SE			77.3

Table 4. Species unique to each region, and to the two geographically coherent pairs of regions. Asterisked species are extinct on Porto Santo.

SW	NC	SE	SSE	SW and NC	SE and SSE
<i>L. espigaoensis</i> *	<i>C. calculus</i>	<i>A. gracilis</i>	<i>D. bulweri</i>	<i>C. mucronatum</i> *	<i>D. oxytropis</i>
<i>P. pygmaeum</i> *		<i>D. rotula</i>	<i>D. cockerelli</i> *	<i>L. subcorneocostata</i> *	<i>L. wollastoni</i>
<i>P. placida</i> *		<i>D. bicarinata</i>		<i>C. compactus</i> (large)	
<i>P. crassus</i> *		<i>L. webbiana</i>		<i>A. crassiuscula</i> *	
<i>A. cf. cimensis</i>				<i>D. attrita</i>	
<i>G. acarinata</i> *					
<i>C. hartungi</i>					
<i>A. morenensis</i> *					
<i>Leptaxis</i> sp.*					

there are 47 species (still excluding S2), of which 16 are extinct (34.0%). At the other end of the scale, no Holocene deposits were

sampled in the SSE region (Site 12). Only two species were unique to the region (Table 4), and only one of these is extinct (*D. cockerelli*).

Table 5. Temporal distribution of native species. Species extinct on Porto Santo are asterisked. Note that for extant species only the fossil ranges are shown. Species with a question mark against them are known from S2, but from no samples with A/I ratios <0.7. Otherwise, all sites except S1 and S2 are included.

Species	>0.7	>0.4	>0.2	<0.2	Species	>0.7	>0.4	>0.2	<0.2
<i>C. mucronatum</i> *	x	x	x		<i>C. s. subcalliferus</i>		x	x	x
<i>T. linearis</i> *	x	x	x		<i>C. hartungi</i>		x	x	x
<i>S. saxicola</i> *		x			<i>C. calculus</i>		x	x	
<i>L. subcorneocostata</i> *	x				<i>C. punctulatus</i>	x	x	x	x
<i>L. espigaoensis</i> *	?				<i>C. bowdichianus</i> *	x	x	x	x
<i>L. monticola</i>	x	x	x		<i>A. arcinella</i> *	x	x	x	x
<i>L. calathiscus</i>			x		<i>A. crassiuscula</i> *	x	x		
<i>P. pygmaeum</i> *	?				<i>A. effugiens</i>	x	x	x	x
<i>P. placida</i> *	?				<i>A. morenensis</i> *	?			
<i>P. crassus</i> *	?				<i>D. rotula</i>		x	x	x
<i>P. portosanctanus</i> *	?	x	x	x	<i>D. bicarinata</i>				x
<i>A. melampoides</i>	x	x			<i>D. b. aucta</i> *	x	x	x	
<i>A. triticea</i>	x	x	x	x	<i>D. oxytropis</i>		x	x	
<i>A. oryza</i>	x	x	x		<i>D. cheirantocola</i>	x	x	x	x
<i>A. gracilis</i>				x	<i>D. calcigena</i>		x	x	
<i>A. cf. cimensis</i>	?				<i>D. pulvinata</i>		x	x	
<i>C. ovuliformis</i>	x	x	x		<i>D. attrita</i>	x	x	x	x
<i>B. lowei</i>	x	x	x		<i>D. bulweri</i>		x	x	
<i>H. paupercula</i>	x	x	x	x	<i>D. cockerelli</i> *		x		
<i>G. coronata</i>	x	x	x	x	<i>D. tectiformis</i>	x	x	x	x
<i>G. acarinata</i> *	?				<i>P. portosanctana</i>	x	x	x	x
<i>S. obtecta</i>	x	x	x	x	<i>P. lowei</i> *	x	x	x	x
<i>S. depauperata</i>	x	x	x	x	<i>Leptaxis</i> sp.*	?	x		
<i>C. compactus</i> (large)	x	x	x	x	<i>L. chrysomela</i> *		x	x	x
<i>C. compactus</i> (small)	x	x	x	x	<i>L. cf. fluctuosa</i> *	x	x	x	x
<i>C. cf. compactus vigiae</i> *	x	x	x	x	<i>L. nivosa</i>	x	x	x	x
<i>C. consors</i>		x	x	x	<i>L. wollastoni</i>		x	x	x
<i>C. abjectus</i> agg.	x	x	x	x	<i>L. webbiana</i>		x	x	
<i>C. subcalliferus submajor</i> *	x	x	x	x	<i>H. subplicata</i>	x	x	x	x

The distinctive environmental division is at A/I 0.2–0.4, corresponding to the last cold period of the Pleistocene. The earlier section spans a much longer period including both warm and cold phases, while later samples come from the warmer part of the Holocene. In terms of presence and absence, there is no significant difference between the two pre-Holocene periods. Quantitative differences between the three temporal divisions in the five major GAG sites reveal no consistent patterns; troughs in relative abundance of particular species in some sites are countered by peaks in others. At Site 1 and Site S3, essentially from the same locality, we can compare changes between samples from A/I 0.4–0.7 and those from A/I 0.2–0.4. For the 17 species common to both sites in these age ranges, eight show concordant changes in relative frequency, and nine are discordant. In the best quantitative series from Site S3 there is much variation between samples in species proportions, but the only evident temporal trends are the relative reduction of large *C. compactus* agg. in the cold phase (A/I 0.2–0.4), accompanied by the first appearance of the extinct small *C. compactus areiensis*.

Changes with Time: Regional Patterns

As shown above, there are regional differences between faunas. Table 6 shows spe-

cies richness data in the sites with more than two samples, ordered by the A/I divisions. Overall, the data show that, in early times, regional faunas were similar in richness though differing in composition, but later the fauna of the SW, and to a lesser extent that of the NC, declined, while that of the SE remained high, with some turnover in species composition. Seven out of nine extinct species survived into the Holocene at Site 2; four out of ten did so at Site 1, but only two out of ten did so at Site 7. At Site S3 (NC), there are no Holocene samples, but 10 out of 11 extinct species survived there into the last glacial (A/I 0.2–0.4).

The modern fauna of the island is now very well known (Cameron et al., 1996b; Seddon, in press). It is therefore possible to compare past and present distributions of extant taxa. The following patterns occur:

Continuously Broad Distribution: There are numerous species in this category, for example, *Heterostoma paupercula*, *Boettgeria lowei*, *Leptaxis nivosa*, *Spirorbula oblecta*, *S. depauperata*, *Caseolus punctulatus* and *Discula tectiformis*. Some of these are missing from the more grossly disturbed areas today.

Continuously Restricted Range: A number of species with restricted eastern distribution today seem to have been so restricted through

Table 6. Species richness and sample sizes, by A/I divisions, for the sites containing more than two samples. Unique indicates species confined to that division within the site.

Region/Site	>0.7	>0.4	>0.2	<0.2	Total	Region/Site	>0.7	>0.4	>0.2	<0.2	Total
SW Site 7						NC Site 1					
Samples	4	2	2	1	9	Samples	4	2	2	2	10
Shells	1310	266	454	526	2557	Shells	1329	248	156	388	2121
Species	30	15	14	13	32	Species	25	20	14	16	29
Extinct	10	5	2	2	10	Extinct	9	7	4	4	10
Unique	12	0	2	0		Unique	7	0	0	2	
SW Site 6						NC Site S3					
Samples		6	2		8	Samples	5	2	4		11
Shells		1261	354		1615	Shells	669	300	861		1830
Species		21	14		22	Species	21	20	26		31
Extinct		5	4		5	Extinct	6	6	10		11
Unique		8	1			Unique	1	1	6		
SSE Site 12						SE Site 2					
Samples		5	1		6	Samples		8	2	6	16
Shells		784	164		948	Shells		1494	254	775	2523
Species		28	24		33	Species		31	27	26	36
Extinct		5	3		7	Extinct		8	7	7	9
Unique		9	5			Unique		6	0	4	

the period covered by our samples. *Lampadia webbiana* occurs only at Site 2, near its modern location on Pico do Concelho, and *Discula oxytropis* only at Sites 2 and 12. *Leptaxis wollastoni* was recorded as abundant by Wollaston (1878) on Pico do Concelho, and it has been found there more recently by Hemmen & Groh (1986), but is unknown elsewhere, other than on the remote Ilhéu de Fora to the northeast. It is present fossil at Site 2 nearby. *Discula rotula* and *D. bicarinata* have somewhat more extensive distributions in the east of the island only and are fossil at Site 2. *D. bulweri*, recorded at Site 12, is also limited to the east. *D. calcigena* occurs everywhere except the NE both as fossils and in modern faunas. At the western end of the island *Leiostyla subcorneocostata* is present in early horizons at Site 7, in Site S2, and in one of Seddon's samples from Fonte da Areia (Site S3). It appears always to have been rare. The very similar *L. corneocostata* lives today at the southwestern tip of the island near Site 7.

Reduction of Range: Apart from outright extinction, the most dramatic reductions in range and abundance are shown by *Geomitra coronata*, abundant in the fossil record, but now confined to two widely separated localities, and *Helix subplicata*, not as abundant, but widespread, which is now confined to the offshore islet Ilhéu do Baixo in the southwest. *Pseudocampylaea lowei*, once widespread, but now extinct, survived into the 20th century on Ilhéu de Cima in the SE, while *P. portosanctana*, once widespread, now has a disjunct distribution, mainly on offshore islets (Cameron and Cook, 1996). *Discula attrita*, now mainly on Pico da Ana Ferreira, is present throughout Sites 7, 6 and 1. *Amphorella triticea* was recorded at all fossil sites but is now an eastern species only. *Caseolus consors* and *Discula cheiranticola* also occur as fossils in the SW and NE, but are now confined to the east.

Expansion of Range: Modern endemic species not found in the fossil record were considered earlier. It seems unlikely that their ranges have increased significantly. *Caseolus hartungi*, however, is widespread (mainly coastal) today but occurs very rarely, and in small numbers, in fossil samples from the SW only.

Change of Location: *D. pulvinata* is now established near Site 1 and is present only in the youngest Site S3 samples from this area.

It is not now known from near Sites 2 and 7 where it occurs as a fossil.

Morphological Variation

Fossil snails are, necessarily, identified by shell characters, and those that are extinct can only be described from such characters. Some species have "forms" or subspecies known only as fossils. The fact that there may be variation in time adds to the problems of determination. Amongst the many morphometric studies that could be made using our material, we have undertaken three, illustrating different aspects of variation.

(1) Variation in *Heterostoma*. A small discoidal helicid with a down-turned mouth, unlike anything else on the islands, occurs on all three Madeiran groups. It is referred to here as *Heterostoma paupercula* (Lowe, 1831). Since Lowe's time it has been divided into three species in two genera on the basis of size, shell sculpture and colour, presence or absence of a tooth in the aperture and presence or absence of an epiphallus. When these distinctions were made (Mandahl-Barth, 1943), *H. paupercula* was redefined as hemiphallic, with a toothed aperture and small, granular and brown shell. A new genus *Steenbergia duplex* was euphallic, with no tooth and a paler shell with larger granules. Two subspecies were named, which differed in size and location, later regarded as separate species by Waldén (1983). Even at that time it was apparent that the characters do not associate consistently (Backhuys, 1975; Waldén, 1983; Lace, 1992; Cameron et al., 1996a), so that for practical convenience we have used the original name. Lace (1992) studied animals from the three island groups within the archipelago. She found considerable variation in size and proportions of genitalia throughout the range. On Ilhéu Cima, at the eastern end of Porto Santo and the neighbouring mainland in the region of the present Site 2 the populations contained small, euphallic toothed individuals and larger hemiphallic individuals lacking the tooth. Studies of isozymes showed that there was reduced heterozygosity and similar but different frequencies of alleles in the two types. Cook & Lace (1993) suggested that the hemiphallic individuals might be part selfing, part female, while the euphallics are cross-fertilizing. Craze & Lace (2000, 2002) found populations composed entirely of hemiphallics, which is not

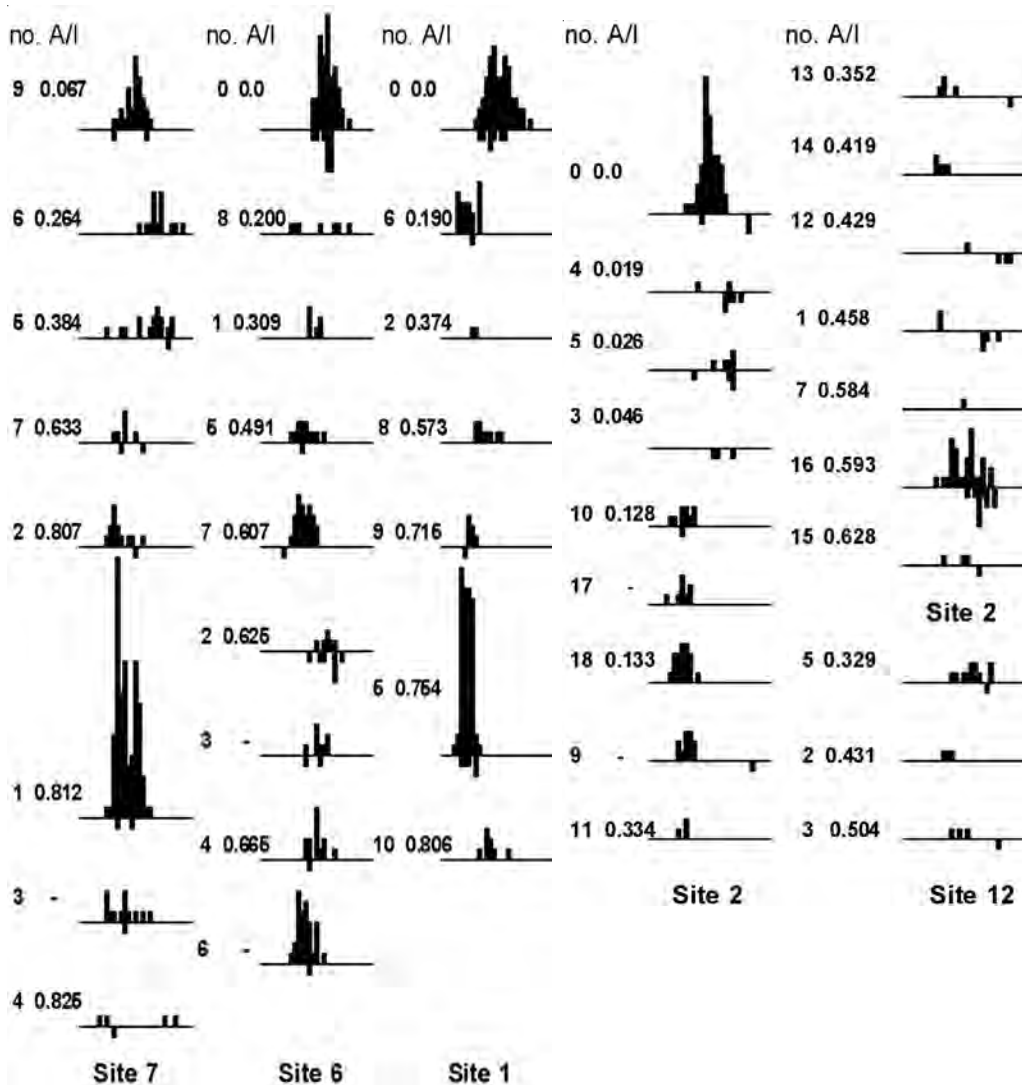


FIG. 4. Shell breadth in *Heterostoma paupercula* from the five sampled sites. Left: from SW and NC, right: samples from SW. Shells measured to 0.1 mm; range shown is 3–6 mm. Toothed individuals above horizontal line, untoothed individuals below line. Samples given an A/I ratio of 0.0 are modern.

possible if they simply act as females, and molecular differences between hemiphallics and euphallics. The different types may therefore be separate sympatric species, although the possibility that the genetic differences are due to partial selfing has yet to be excluded. Elsewhere on Porto Santo untoothed shells are euphallic and the same size as toothed (Lace, 1992; Cameron et al., 1996a). Frequency of tooth presence, shell size and colour

vary in a seemingly irregular manner from sample to sample. The relations now seen in the eastern region appear to be limited to it.

In order to examine whether these patterns of distribution also occur in the fossil sequences, and whether any changes have taken place, all shells from the samples have been measured and scored for presence or absence of tooth. Shell colour proved impossible to score. The results are summarized as

a series of histograms (Fig. 4). At Sites 7, 6 and 1 untoothed individuals are present but quite rare (6.6% over all fossil samples) and are as likely to be smaller as larger than toothed individuals. Untoothed individuals are more common (23.4%) in the long series from Site 2. They are usually larger than toothed individuals, especially in the early part of the sequence. The mean breadth in the toothed samples appears to drop from 2-16 ($A/I = 0.593$) to 2-10 ($A/I = 0.128$), and after the gap at 2-3 to increase. The majority of individuals in 2-1 and 2-12 (A/I 0.429, 0.458) are untoothed and large. Since mean breadth varies from sample to sample significance tests have been carried out within samples and combined. Taking only samples where there

are at least two untoothed individuals the trend obtained by combining samples from Sites 7, 6 and 1 gives a normal deviate of 0.62, which is not significant. For Site 2 the normal deviate is 7.20 ($P < 0.001$), supporting the difference apparent in the diagrams. The present pattern, in which samples with large untoothed and small toothed shells are restricted to the SE, was therefore present throughout the recorded history of *Heterostoma*.

(2) *Spirorbula depauperata* and *S. latinea*. Wollaston (1878) listed three *Spirorbula* species for Porto Santo. One, *S. obtecta*, is clearly distinct, but the extinct *S. latinea* and the extant *S. depauperata*, which is also found as a fossil, are very similar. Examination of the type

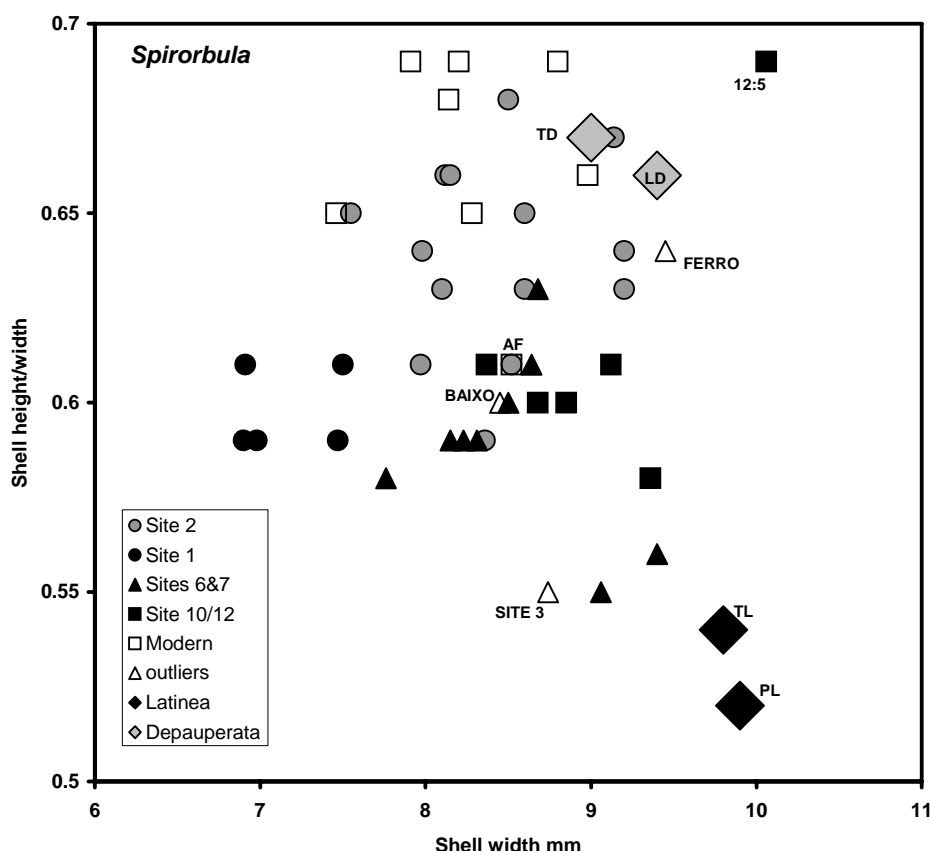


FIG. 5. The relationship of mean shell width and shell height/width ratio for samples of *Spirorbula depauperata/latinea*. For locality symbols, see inset. Diamonds indicate the positions of type specimens (TD = type of *S. depauperata*; TL = type of *S. latinea*), and of other samples made by the species' authors (LD = Lowe, *S. depauperata*; PL = Paiva, *S. latinea*). AF indicates the position of a modern sample from Pico da Ana Ferreira. Fossil samples from minor sites labelled.

specimens alone suggests that the distinction is relatively easy to make. However, examination of our material and of modern samples of *S. depauperata* shows that this is not the case. Fig. 5 shows the relationship between shell size and shape for the types, for museum lots collected in the nineteenth century, and for recent and fossil samples made by us. The whole range of shapes is found. There is evidence of geographical variation in size and shape among fossil samples, but no consistent trends with time within each site (data not shown). The types and early collections lack precise locality data. All but one of the modern samples come from the east, and they overlap with fossil samples from Site 2. The outlying position of the sample 12-5 is discussed further below.

(3) Variation in *Discula oxytropis*. The modern form of this species is restricted to the south-eastern part of Porto Santo. Wollaston (1878) described a variety (*α subcarinulata*), common as a fossil, characterised by larger size and relatively higher spire. He also noted the fossil occurrence of *D. vermetiformis* (Lowe, 1854) as a closely related species characterised by a double keel, a character that it shares with *D. bicarinata* and its close relatives. Waldén (1983) treated both these as extinct subspecies of *D. oxytropis*. Fig. 6 shows the relationship between shell size and shape, and the extent of double keeling, for the types and other old museum collections, and for fossil and modern samples made by us. Early samples are not localised; our own fossil material comes only from the east, in or

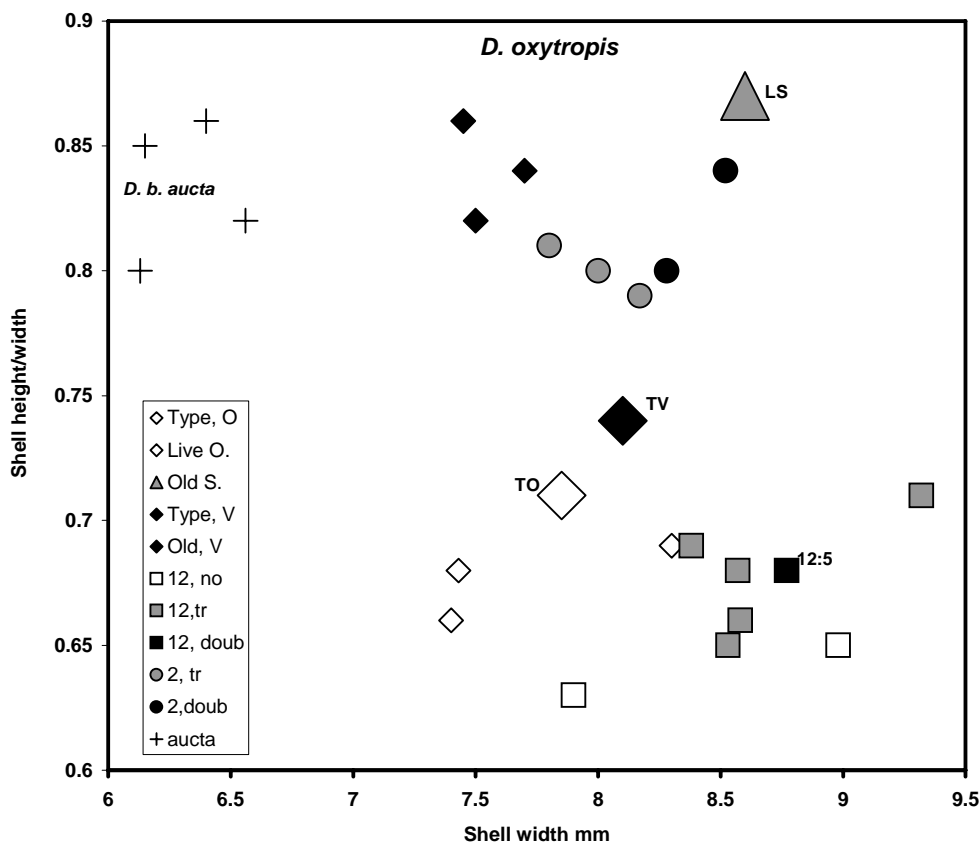


FIG. 6. The relationship between mean shell width and shell height/width ratio for samples of the *Discula oxytropis* group. For symbols, see inset (T = type specimen; L = sample labelled *subcarinulata* by Lowe; O = *D. oxytropis*; V = *D. cf. vermetiformis*; S = *D. cf. subcarinulata*). Open symbols, single keel; grey symbols, trace of second keel; black symbols, double keel. The crosses show the position of fossil samples of *Discula bicarinata aucta* (see text).

near the present distribution. The figure also shows the same data for fossil samples of *D. bicarinata aucta*, the form Wollaston regarded as the closest to *D. vermetiformis*.

As with *Spirorbula* above, consideration of many samples blurs the apparently clear separation suggested by the types. At Site 12, the whole range from clearly single to clearly double keeled specimens can be found, and, again, sample 12-5 is distinctive. Given that Site 12 samples were scattered, and not in a single stratigraphical column, we suspect that 12-5 represents a distinct fauna. The modern distribution of *D. oxytropis* is in much the same area. Samples from Site 2, nearby, generally resemble the old sample of *D. o. subcarinulata* to a greater extent, with mixed expression of keeling, while the nineteenth century collections labelled *D. vermetiformis* resemble *D. o. subcarinulata* in shape more than does the type. *D. bicarinata aucta* seems clearly distinct on the basis of size. Shape appears to vary geographically, while keeling is idiosyncratic. In neither case is there any consistent relationship with age, except that all modern shells are single-keeled and relatively low spired.

DISCUSSION

The reasons for high diversity and rapid evolution on islands are still incompletely understood. Our survey of extant faunal distributions in the Madeiran archipelago has been directed at these problems. Knowledge of the fossil associations adds a historical dimension. Results presented here suggest that faunas on Porto Santo and Madeira have responded differently to past climatic change, that there have been different levels of extinction and that different island topography provides a central explanatory factor.

Stasis and Change

The predominant impression is one of stasis, even at regional level within the island. Not only do the most abundant species remain dominant throughout the sequences, but it is also hard to relate extinctions and fluctuations in abundance to known climatic variation in the Quaternary. Only comparison of the fossil fauna as a whole with the modern one shows profound change. Even then, geographical distributions remain unchanged in many species, and in others reduction in modern range

can be attributed to human disturbance. The morphometric studies support the pattern of geographical and temporal stasis; local differences in character associations in *H. paupercula* are maintained; a geographical pattern of shell shape is maintained in *S. depauperata*, and only in *D. oxytropis* do some characters appear to fluctuate within localities.

In these respects the fossil faunas of Porto Santo differ from those of the only fossiliferous site on Madeira, situated on its eastern peninsula, the Ponta de São Lourenço (Cook et al., 1993; Goodfriend et al., 1994, 1996). On Madeira, there were substantial shifts in relative abundance and occurrence of species with time. In apparently wetter phases, fossil faunas included larger numbers of species that have forest or montane distributions today; in drier phases species characteristic of dry, open and mostly coastal habitats prevailed. The difference between the modern and fossil faunas at the Madeiran fossil site is also far greater: only 12 out of 43 fossil species recorded now live on the peninsula. Of these, two, *Theba pisana* and *Cochlicella barbara*, are introduced species present only in samples from post-colonisation horizons.

The Madeiran fossil sequence spans a shorter period, most samples being from the Holocene, and most earlier ones from either the last interglacial or a warmer interstadial within the last cold phase (approximately 45 ka BP; Cook et al., 1993). Cold-phase conditions correspond to periods of rapid sand accumulation and an absence of snail fossils, a situation not evident on Porto Santo. Within the Holocene, but prior to human colonisation, there is a small shift from open to woodland species, terminated abruptly and reversed in post-colonisation samples. The very oldest samples (135+ ka) cannot be assigned to particular Pleistocene conditions; they have open habitat species comparable to those in post-colonisation samples. There are no natural forests surviving on Porto Santo and little indication as to what pre-colonisation vegetation was like, though it is clear that there was at least some tree and shrub cover. Three species fossil and extinct on Porto Santo are found today in forest faunas on Madeira: the endemic *C. mucronatum*, and the non-endemic but native *P. pygmaeum* and *P. placida*. They occur together in Site S2, suggesting a forested habitat, although in company with *S. saxicola*, also extant on Madeira, which is primarily an open habitat species.

Altogether, the evidence from this analysis suggests that the Porto Santan fauna remained, until human colonisation, much more stable through the late Pleistocene and Holocene than the equivalent fauna of the eastern peninsula of Madeira, which today resembles Porto Santo in substrates and habitats. There are no clear signals of response to climatic or habitat change.

Extinctions and Appearances

Cameron & Cook (1996, 1999) reviewed rates and causes of extinction on Madeira, Porto Santo and the Desert Islands. The overall level of extinction of species known as fossils on Porto Santo was 15 out of 54 (27.8%). The present results, including endemics and the two native non-endemics, bring the totals to 25 out of 64 (39%), the increase, influenced slightly by taxonomic decisions, reflecting inclusion of recently described extinct species. The level of extinction is similar on Madeira, at 33% (Cameron & Cook, 1996). Two-thirds of this loss is human-induced and thus very recent (Goodfriend et al., 1994). Our dated samples from Porto Santo are mostly pre-colonisation, but because approximately 26% of species known to be present in the Holocene are now extinct, this too suggests a human cause.

In the case of Porto Santo we have a spread of geographical as well as temporal variation in composition. Impoverishment and extinctions appear to start well before the Holocene, largely due to a marked early decline in the SW, where a number of species unique to that region disappeared quite early in the sequence. Whereas in fossil samples, especially in early ones, the SW is the richest region, in the modern fauna the situation is reversed: the east has more restricted species and richer faunas than to the west (Cameron et al., 1996b). Today, the greater heights and extent of the eastern hills, and the larger areas free of mobile sand, make this difference understandable in terms of refugia and range of habitats. While we lack very early samples from the SE and SSE regions, those from the NC region, including some of the earliest in our array, maintain high levels of richness until the Holocene, but lack a significant suite of unique species as once found in the SW.

On Porto Santo, very few species are missing from the earliest major temporal division ($A/I > 0.4$). All are small and are rare in the

samples and their absence may well be due to sampling error. On Madeira, however, a significant number of species appear for the first time relatively late in the sequence, and in sufficient numbers to suggest that we are not dealing with sampling artefacts. Thus, for example, *H. paupercula* and *C. bowdichianus*, found throughout the Porto Santan series, do not occur until the Holocene on Madeira, and several other, later abundant, species such as *Geomitra delphinula*, *Spirorbula squalida*, *Actinella promontoriensis* and *Discula polymorpha* are missing from the earliest samples (before approximately 135 ka), and are very rare before the Holocene. The last, a very close relative of *D. calcigena* on Porto Santo, is particularly interesting, as it is typical of open, dry habitats of the kind indicated as being represented by the earliest Madeiran samples. Because there is a long temporal gap, from approximately 8 ka to approximately 45 ka, in the Madeiran sequence, the timing of these arrivals remains uncertain, but Porto Santo is a likely source, especially for *C. bowdichianus* and *H. paupercula*. There are very few extant native species in common between the two islands, and a different balance of genera and species richness within each (Seddon, in press). The similarity is slightly greater when extinct species are considered, a point first made by Charles Lyell in a letter to Wollaston in 1856 (Wilson, 1970). The depth of sea between the two islands would seem to exclude a land connection at any time, but there has been a continuing, if very small exchange, some effects of which have been removed by human-induced extinctions.

Patterns and Topography

Porto Santo is an older island than Madeira. Volcanic activity ceased at least 8 million years ago, the topography became strongly eroded and extensive wind-blown deposits have accumulated. This contrasts with Madeira, where there have been repeated phases of vulcanism, possibly down to a quarter of a million years ago, with lava sometimes occupying existing river valleys (Nascimento Prada & Serralheiro, 2000). Unlike Madeira, where coasts shelf steeply into deep water, Porto Santo is surrounded by a substantial platform of shallow sea. At Pleistocene low sea levels most of this was exposed to make the island at least three times its present size and include the offshore islets (Seddon, 1995). Con-

sidering the patterns of distribution in the modern fauna, Cameron et al. (1996b) suggested that small-scale allopatric divergence had resulted from periodic bursts of sand mobility, which isolated populations on the rocky hills. Changes in sea level that were probably the trigger for sand mobility, would isolate and reconnect offshore islets. Human disturbance has mimicked these effects, producing some vicariant distributions (Cameron & Cook, 1996). The results reported here show the time scale to be long, since the patterns in the modern fauna are mostly repeated in the fossil faunas. This reflects a growing consensus that, away from the immediate proximity of glaciers, differentiation of modern faunas started quite early in the Pleistocene (Weir & Schluter, 2004).

On Madeira there is a sharp contrast between relatively undifferentiated forest faunas and those from drier coastal scrub, which have a number of geographically distinct species associations, including replacing sister species (Cameron & Cook, 2001). The differences between forest and coastal scrub are deep, reflecting differential colonization or perhaps an early evolutionary radiation. As on Porto Santo, geographical differentiation in the open, coastal environments can be explained by periods of isolation. These could result from volcanic activity, extension of the forest zone to sea level during colder or wetter phases and/or sea level change during the Pleistocene. The isolating processes appear to have modified the structure of the islands at rates that happen to match rates of dispersal of taxa in such a way as to facilitate evolutionary divergence.

The large changes in faunal composition in the Madeiran fossil deposit, compared with those on Porto Santo, are noteworthy because the fossil site has no high mountains nearby, and is by far the driest part of the island, yet contains species with modern high montane distributions. Some open country species may be late arrivals from Porto Santo. That they did not arrive earlier might be chance; it might also indicate that earlier environments were unsuitable. Present climate and habitat is very similar to that of Porto Santo, so that, given the present topography, it is hard to see why it should have differed radically in the past.

We are left, therefore, to discover some other event or circumstance unique to one or the other island. One possibility is that the extreme east of Madeira has altered radically within the

period covered by the fossil record. The north side of the Ponta de São Lourenço is a set of sheer cliffs descending into a deep-sea trough between Madeira and Porto Santo. The peninsula forms part of a ridge connecting Madeira to the Deserta Islands, the intervening part of which is now submerged, and it seems likely that submergence is a product of erosion or collapse as much as of changing sea levels. This ridge and the Desertas as a group are products of relatively recent volcanic activity. They rise from great depths on either side, and are remnants of a larger landform. At least one massive landslide has occurred on Deserta Grande in recent times, causing a minor tsunami in Funchal, the capital of Madeira. The Desertan snail fauna has many species in common with that of Madeira (Cameron & Cook, 1999). A greater and higher land mass rising on the north side of the peninsula but now lost by slumping could explain the past occurrence of montane and forest species on the peninsula. By comparison, no such events would have taken place on Porto Santo in the same time frame because of its position on a shallow submarine plateau.

Equally puzzling is the early impoverishment of faunas in the SW of Porto Santo. This could be due in part to the small number of samples and sites investigated in a widespread and complex series of deposits. We cannot help noticing, however, that the area concerned lies directly in the path of any tsunami emanating from a large scale collapse at the eastern end of Madeira, neatly complementing the suggested change there.

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- 8-1. Clayey colluvium, slightly indurated. Sample taken of material between 32 and 45 cm from top of a gully exposure 65 cm deep.
- 8-2. Friable clay deposit, eroded to seaward. Sample from material 10 to 35 cm below top of unit, which is capped by a red buried soil.
- Site 3. One locality at Ponta da Calheta (718549).
- 3-1. Sample 40 to 80 cm below the top of a 3.5 m deep deposit of amorphous carbonate-rich sand resting on volcanic bedrock. Above this deposit is a car park and recently disturbed material.
- Site S2 (approximately 715556) about 1 km NE of Porto da Morena.
- Samples S2-2 and S2-3 come from a 3.5 m deep exposure of colluvium on the NW side of a small valley. There are two units: a lower (2.2–3.5 m) one of yellow sand, in which S2-3 was made in the top 50 cm, and an upper (0–2.2 m), in which S2-2 was made in the central 1 m portion. S2-1 was made from an extension of this upper unit, approximately 300 m away
- Site 7* (700563). Eroded slopes facing south to Ponta da Canaveira.
- Samples 7-1 to 7-5 come from a single, trackside exposure approximately 18–20 m deep. There are two units. The lower one, resting on bedrock, varies between 3.5 and 5 m deep, is colluvial, and varies in texture from brown-red clays to patches with many rocky inclusions. 7-1 and 7-2 come from 50 cm vertical sections near the base of this unit, and 7-3 from a 25 cm section starting 75 cm from its top. The upper unit, approximately 15 m thick, is sandier, with later fissure fills. 7-4 is a 40 cm section starting 80 cm from the base of this upper unit, and 7-5 a similar section starting 3.1 m above the base of this unit. A/I ratios indicate that 7-1, 7-2 and 7-4 are all much the same age, and very old, whereas 7-5 is much younger. The remaining samples (7-6 to 7-9) come from separate exposures slightly higher up the valley, and we cannot integrate their stratigraphical details. On A/I ratios, 7-7 and 7-8 are older than 7-5, but younger than 7-1 to 7-4. 7-6 and 7-9 are much younger.

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APPENDIX 1

Details of the sites used in this study. The sequence retains GAG numbering, and numbers assigned to MBS sites, and run clockwise from the extreme SW (Ilhéu de Baixo). Site locations are shown in Fig. 1. Grid references are provided using the grid on the 1970 1/50,000 map published by the Portuguese Instituto Geográfico e Cadastral. Asterisked GAG sites are those with more than two samples, which are subject to detailed analyses.

Southwest Region (SW)

Site 8. Two localities on Ilhéu de Baixo (approximately 709525).

Site S1 (700563). Ponta da Canaveira.

Samples taken from a 19 m deep exposure of calcarenite with interbedded layers of sand

or silt. S1-4 comes from near the base of this sequence (18.0–18.1 m), in a breccia containing shells and volcanic clasts. S1-3 (16.0–16.5 m) comes from a bed of consolidated yellow sand. S1-2 comes from a narrow band of silt at 5.45–5.50 m. S1-1 was made at the same depth, but from a short band of blown sand.

Site 11. Ilhéu de Ferro (689560).

Single sample collected by excavation from a approximately 30 cm thick band of indurated clay exposed by erosion. This sample is undated.

Site 6*. West-facing slopes of Espigão (705564).

Samples 6-1 to 6-5 come from the slope of an eroded gully, exposing approximately 7 m depth of sediments. Three units were distinguished. 6-5 represents picked shells from a band 10 cm deep, just below the top of the basal, red sandy clay unit, of which only approximately 30 cm were exposed. 6-4, 6-3 and 6-2, each approximately 50 cm deep, come, respectively from very near the base, two thirds of the way up, and just below the top of the middle unit, approximately 6 m depth of largely unbedded sands, slightly indurated, with evidence of later fissure fill near the top. 6-1, 30 cm deep, represents the whole thickness of the uppermost unit, which consisted of clayey sand, darker in colour than the sands of the unit below. A/I ratios for 6-4 and 6-2 are very similar, suggesting that the middle unit accumulated very rapidly. Some A/I values for 6-5 are anomalous, but the largest are similar to those of 6-4 and 6-2. 6-6 and 6-7 come from a much smaller exposure within 50 m of the previous one. 6-7 represents picking from a section 10 cm deep, 10 cm from the top of the lowest unit exposed (80 cm), which is traceable to the unit containing 6-5 (A/I determinations confirm this). 6-6 comes from a 30 cm deep unit of red clay immediately above the unit containing 6-7. No A/I determination is available for this sample. It appears to be stratigraphically equivalent to the unit containing 6-4 to 6-2, but the unit differs radically in thickness and composition. 6-8 comes from a road cut exposure, again close to samples 6-1 to 6-5. It represents the upper portion of a 50 cm deep unit traceable to the unit containing 6-1, and with the same character.

Site 9. Road cutting on slopes of Espigão, approximately 500 m inland from Site 6 (710561).

A single sample, picked out between 45 and 75 cm below the top of a 0.8 m deep exposure of loose, sandy colluvium resting on volcanic bedrock. There are no A/I data for this sample, but the presence of *Theba pisana* suggests that it is late, probably post 1420 AD.

Site 4. Eroded deposits above sea-cliffs at São Sebastião (718580).

Sample 4-1 comes from the bottom 10 cm of a 3 m unit of bedded and partly indurated sand, which overlies a layer of brown blocky clay containing concretions. A/I data indicate a similar age to the oldest samples from Site 6. 4-2, for which there is no A/I data, comes from a nearby exposure, but from the top 10 cm of a much younger deposit, probably similar to that containing samples 6-1 and 6-8.

North-Central (NC)

Site 5. An exposure at the bottom of a gully on the north side of Barbara Gomez (727602).

Goodfriend identified here a sequence of six well-stratified units exposed over approximately 6 m depth, and clearly earmarked the site for further work. 5-1 comes from the top of the uppermost unit; 5-2 spans 30 cm depth, 90 cm below the top of the fifth unit down. Many intervening units are marked as holding shells. A/I data for 5-2 equates it with 4-1, and with the earliest samples from Site 6. There are no A/I data for 5-1, but the stratigraphy suggests that it is much younger. It also contains *Theba pisana*. It should be noted that this site contains only species common to both SW and NC regions.

Site 1* (approximately 729613). Exposures in erosion surfaces and road cuttings at Fonte da Areia.

The main sequence of samples here can be related to a section varying in depth, but generally 30 m or more. This section is multi-layered, with a number of narrow calcrete bands within it. The basal 10 m appeared not to contain shells. All samples except 1-6 and 1-7 came from this section. Figure 3 compares the stratigraphical positions of samples in this series with the range of A/I values. Samples 1-1, 1-2, 1-8, 1-3 and 1-10

show a coherent pattern, with only typical variation (Fig. 2) between individual A/I values. 1-5, 1-4 and 1-9 have wide ranges of A/I values (some of them extreme, $A/I > 1.0$), and the mean A/I values run counter to their stratigraphical position. The lowest sample, 1-5, comes from a dense accumulation of shells, clearly washed together. There appears to have been significant mixing and reworking of deposits in this sequence. Samples 1-6 and 1-7 come from exposures above, and 100–200 m away from the main section. They have similar, low A/I values, and, on topographical grounds, are probably aeolian deposits.

Site S 3. Fonte da Areia.

This section was made very close to the main sequence of Goodfriend. No A/I data are available for these samples, but it is possible to match up the stratigraphical diagrams with some confidence. They span the same depth, and have some well defined calcrete layers at approximately the same intervals. These are used to align the sequences as shown in Fig. 3. Other discontinuities, also shown, are impossible to align with certainty.

Southeast Region (SE)

Site 2* (centred on 792594).

Samples from this site come mainly from coastal and road cut exposures through sandy deposits at Calhau da Serra de Fora/Porto dos Frades. Many samples are single

removals from particular exposures, and cannot be directly correlated with strata elsewhere; A/I values are the only means of ordering them. In particular cases where several samples come from a single stratigraphical column, the agreement is good (2-3 to 2-5; 2-9 to 2-12; samples 2-15, 2-16 and 2-7 were identified as coming from the same stratigraphical unit).

South-Southeast Region (SSE)

Site 12* (including Goodfriend's Sites 10 and 13) (788587).

Samples come from clay and rocky colluvium along the coast between the new harbour (Peneda) and Pedras Altas immediately below Pico do Baixo. The deposits were impossible to align along this coast, due to strong dipping and inconsistent colouring, the material coming from steep hill slopes above, of varying character. 12-2 was 1.5 m above 12-1 in the same section, but has a very slightly larger mean A/I ratio. 12-1 to 12-4, and 10 all came from near the base of exposed sediments. 12-5 was collected higher up relative to sea level; above it was an unsampled unit containing *Theba pisana*. The limpet shells (Site 13) from the basal calcrenites just above sea level give a mean A/I ratio only marginally larger than those from some of the overlying colluvial deposits. It would appear that these deposits accumulated rather rapidly; the range of A/I values here is small.

APPENDIX 2

Taxa recorded in Site 7, samples arranged by A/I ratio and stratigraphical position. Note that, at this site, there is some discordance between the two (see Appendix 1).

A/I Species/Samples	0.825 4	0.812 1	n/a 3	0.807 2	0.69 8	0.63 7	0.384 5	0.264 6	0.067 9
<i>Craspedopoma mucronatum</i>									
<i>Truncatellina linearis</i>		3				1			
<i>Staurodon saxicola</i>									
<i>Leiostyla subcorneocostata</i>		23	1	1					
<i>Leiostyla calathiscus</i>									
<i>Leiostyla monticola</i>									
<i>Phenacolimax portosanctanus</i>									

(continues)

(continued)

A/I Species/Samples	0.825 4	0.812 1	n/a 3	0.807 2	0.69 8	0.63 7	0.384 5	0.264 6	0.067 9
<i>Amphorella melampoides</i>		11		4					
<i>Amphorella triticea</i>			2						
<i>Amphorella oryza</i>		6		5					
<i>Amphorella gracilis</i>									
<i>Cylichnidia ovuliformis</i>		12							
<i>Boettgeria lowei</i>		11	1	7					
<i>Heterostoma paupercula</i>	5	124	15	16	1	9	20	17	37
<i>Geomitra coronata</i>		67	50	19	1				30
<i>Spirorbula oblecta</i>		11	6	1			2	2	
<i>Spirorbula depauperata</i>	5	34	20	11	21	21	2		1
<i>Caseolus compactus</i> (large)	4	7	20	2	1		8		
<i>Caseolus compactus</i> (small)	23	114	86	21	18	40	29	13	72
<i>Caseolus compactus vigiae</i>	8				7	1			9
<i>Caseolus consors</i>								5	
<i>Caseolus abjectus</i> agg.	2	157	25	33	6	10	2		53
<i>Caseolus subcalliferus submajor</i>	10	12	14	8	17	27	21	19	15
<i>Caseolus s. subcalliferus</i>									
<i>Caseolus hartungi</i>									
<i>Caseolus punctulatus</i>	21	54	4	6	31	16	28	19	106
<i>Caseolus bowdichianus</i>	5		5	1	3	4			
<i>Actinella arcinella</i> pap.	1								
<i>Actinella crassiuscula</i>		14	5						
<i>Actinella effugiens</i>		36	4	7		1	1	2	61
<i>Discula rotula</i>									
<i>Discula bicarinata</i>									
<i>Discula bicarinata aucta</i>		21		4					
<i>Discula oxytropis</i>									
<i>Discula cheiranticola</i>	1	1							
<i>Discula calcigena</i>									
<i>Discula pulvinata</i>							77	46	
<i>Discula attrita</i>	1	5	1	2					7
<i>Discula bulwerii</i>									
<i>Discula cockerelli</i>									
<i>Discula tectiformis</i>	1	5		3	10		27	21	27
<i>Pseudocampylaea portosanctana</i>		2		1					26
<i>Pseudocampylaea lowei</i>		10		2					
<i>Leptaxis</i> sp.									
<i>Leptaxis chrysomela</i>									
<i>Leptaxis</i> cf. <i>fluctuosa</i>	1				5		3	4	
<i>Leptaxis nivosa</i>	9	26	1	11	13	2	47	39	82
<i>Leptaxis wollastoni</i>									
<i>Lampadia webbiana</i>									
<i>Helix subplicata</i>		10	1	11					
<i>Theba pisana</i>									
No. of taxa	15	25	18	22	13	11	13	11	13
No. of shells	97	776	261	176	134	132	267	187	526

APPENDIX 3

Taxa recorded at Site 6, samples arranged by A/I ratio and stratigraphical position. GAG data on numbers of *Caseolus bowdichianus* are missing. In sample 5 (asterisked) A/I values were exceptionally variable (Appendix 1).

A/I Species/Samples	0.806 10	0.754 3	0.754* 5	0.715* 9	0.663* 4	0.573 8	0.349 1	0.347 2
<i>Craspedopoma mucronatum</i>								
<i>Truncatellina linearis</i>								
<i>Staurodon saxicola</i>								
<i>Leiostyla subcorneocostata</i>								
<i>Leiostyla calathiscus</i>								
<i>Leiostyla monticola</i>								
<i>Phenacolimax portosanctanus</i>								
<i>Amphorella melampoides</i>								
<i>Amphorella triticea</i>	1							
<i>Amphorella oryza</i>			37		4			
<i>Amphorella gracilis</i>								
<i>Cyllichnidia ovuliformis</i>								
<i>Boettgeria lowei</i>								
<i>Heterostoma paupercula</i>	15	11	33	15	32	15	7	8
<i>Geomitra coronata</i>	1		39		16			
<i>Spirorbula obtecta</i>	14	3	2		4	14	8	14
<i>Spirorbula depauperata</i>	25		11		9			
<i>Caseolus compactus</i> (large)		5	70	22	31		5	3
<i>Caseolus compactus</i> (small)	89	52	54	20	52	56	58	47
<i>Caseolus compactus vigiae</i>								
<i>Caseolus consors</i>								
<i>Caseolus abjectus</i> agg.	10	16	19	2	2	2		
<i>Caseolus subcalliferus submajor</i>	60	30	2	30		3	20	19
<i>Caseolus subcalliferus subcalliferus</i>			3		4			
<i>Caseolus hartungi</i>								
<i>Caseolus punctulatus</i>	20	45	3	30	3	4	23	20
<i>Caseolus bowdichianus</i>	+			+	+	+	+	
<i>Actinella arcinella</i>	24	7	3	1		5	7	4
<i>Actinella crassiuscula</i>						2		
<i>Actinella effugiens</i>	8	1	1	1				2
<i>Discula rotula</i>								
<i>Discula bicarinata</i>								
<i>Discula bicarinata aucta</i>								
<i>Discula oxytropis</i>								
<i>Discula cheiranticola</i>								
<i>Discula calcigena</i>								3
<i>Discula pulvinata</i>								
<i>Discula attrita</i>	11		12		2	5		1
<i>Discula bulwerii</i>								
<i>Discula cockerelli</i>								
<i>Discula tectiformis</i>	3	6		14			28	38

(continues)

(continued)

A/I Species/Samples	0.806 10	0.754 3	0.754* 5	0.715* 9	0.663* 4	0.573 8	0.349 1	0.347 2
<i>Pseudocampylaea portosanctana</i>								
<i>Pseudocampylaea lowei</i>								
<i>Leptaxis</i> sp.								
<i>Leptaxis chrysomela</i>								
<i>Leptaxis</i> cf. <i>fluctuosa</i>	4	5		17	18	1		4
<i>Leptaxis nivosa</i>	29	18	2	6	2		13	22
<i>Leptaxis wollastoni</i>								
<i>Lampadia webbiana</i>								
<i>Helix subplicata</i>			3					
<i>Theba pisana</i>								
No. of taxa	16	12	16	12	14	11	10	13
No. of shells	413	199	294	158	179	107	169	185

APPENDIX 4

Taxa recorded at Site 1, samples ordered by A/I ratio and stratigraphical position. Asterisked A/I values indicate high variability within samples (Appendix 1); + = an approximate number. See Fig. 3.

A/I Species/Samples	0.806 10	0.754 3	0.754* 5	0.715* 9	0.663* 4	0.573 8	0.349 1	0.347 2	0.19 6	0.167 7
<i>Craspedopoma mucronatum</i>	1				2					
<i>Truncatellina linearis</i>		1								
<i>Staurodon saxicola</i>										
<i>Leiostyla subcorneocostata</i>										
<i>Leiostyla calathiscus</i>										
<i>Leiostyla monticola</i>		1								
<i>Phenacolimax portosanctanus</i>										
<i>Amphorella melampoides</i>										
<i>Amphorella triticea</i>		11	42	1	19		1	1	2	
<i>Amphorella oryza</i>				5						
<i>Amphorella gracilis</i>										
<i>Cylichnidia ovuliformis</i>										
<i>Boettgeria lowei</i>										
<i>Heterostoma paupercula</i>		5	166	9	7		2	21	12	
<i>Geomitra coronata</i>		1	90	10	4	3	2	1	7	
<i>Spirorbula oblecta</i>	16		11	1	16			3		
<i>Spirorbula depauperata</i>	3	15	50	5	1	14		3		

(continues)

(continued)

A/I Species/Samples	0.806 10	0.754 3	0.754* 5	0.715* 9	0.663* 4	0.573 8	0.349 1	0.347 2	0.19 6	0.167 7
<i>Caseolus compactus</i> (large)	30			2		2		11		
<i>Caseolus compactus</i> (small)	24	31	300+	29	16	32	1	12	14	97
<i>Caseolus</i> cf. <i>compactus vigiae</i>		1	4	24		27	1	9	7	
<i>Caseolus consors</i>									3	
<i>Caseolus abjectus</i> agg.	39	7	26	8	1	8				
<i>Caseolus subcalliferus submajor</i>		5	5	12	4			5	21	12
<i>Caseolus s. subcalliferus</i>						1		5		
<i>Caseolus hartungi</i>										
<i>Caseolus punctulatus</i>	15	6	15	14	4	30	8	8	45	20
<i>Caseolus bowdichianus</i>	20	6	15	10	15	5	33	13	15	12
<i>Actinella arcinella</i> pap.		5	4	4		6				
<i>Actinella crassiuscula</i>	7	11	2	1						
<i>Actinella effugiens</i>										
<i>Discula rotula</i>										
<i>Discula bicarinata</i>										
<i>Discula bicarinata aucta</i>										
<i>Discula oxytropis</i>										
<i>Discula cheiranticola</i>									1	
<i>Discula calcigena</i>										
<i>Discula pulvinata</i>										
<i>Discula attrita</i>			3	3	3	3	1	3	5	3
<i>Discula bulwerii</i>										
<i>Discula cockerelli</i>										
<i>Discula tectiformis</i>		4	2	5	3	8	21		7	4
<i>Pseudocampylaea</i>	20									
<i>portosantana</i>										
<i>Pseudocampylaea lowei</i>	4									
<i>Leptaxis</i> sp.										
<i>Leptaxis chrysomela</i>						2			28	3
<i>Leptaxis</i> cf. <i>fluctuosa</i>	1	53	5	31	1		10			
<i>Leptaxis nivosa</i>	21	14	8	21	6	5		10	36	5
<i>Leptaxis wollastoni</i>										
<i>Lampadia webbiana</i>										
<i>Helix subplicata</i>		1	5	2						
<i>Theba pisana</i>										
No. of taxa	13	18	18	20	12	17	7	12	16	11
No. of shells	201	178	753	197	60	188	75	81	211	177

APPENDIX 5

Taxa recorded at Site 2, samples arranged by A/I value and stratigraphical position. Samples for which only a few specimens were removed for A/I analysis are omitted.

A/I	0.63		0.59	0.58	0.51	0.46	0.43	n/a	0.42	0.35	0.33	0.13	0.13	0.05	0.03	n/a	0.02
Species/Samples	15	16	16	7	6	1	12	17	14	13	11	18	10	3	5	9	4
<i>Craspedopoma mucronatum</i>																	
<i>Truncatellina linearis</i>																	
<i>Staurodon saxicola</i>																	
<i>Leiosstyla subcorneocostata</i>																	
<i>Leiosstyla calathiscus</i>																	
<i>Leiosstyla monticola</i>		2															
<i>Phenacolinax portosancianus</i>		1	1					1	1	1			1				
<i>Amphorella melampoides</i>	2																
<i>Amphorella triticea</i>	5	42	2				1		3	3	5	1				5	
<i>Amphorella oryza</i>					3												
<i>Amphorella gracilis</i>																	
<i>Cylindridia ovuliformis</i>					1								1				
<i>Boettgeria lowei</i>	1	3	1		11		17		2	8	3						
<i>Heterostoma paupercula</i>	4	41	1		8		4	8	5	5	3	19	13	3	10	14	7
<i>Geomitra coronata</i>	7	29	3		12		7	9	18	5	21	27	12		2	27	1
<i>Spirorbula obtecta</i>	2	9			4		1	13	8	4	7	4	8	2		5	1
<i>Spirorbula depauperata</i>	9	38	4		7		5	8	24	9	21	12	10	5	5	24	
<i>Caseolus compactus</i> (large)																	
<i>Caseolus compactus</i> (small)	39		8	12	21		20	36	24	11	25	63	45		31		2
<i>Caseolus compactus vigiae</i>	11	1	5		2		5	27	10	3	11	21	3	2	5	31	
<i>Caseolus consors</i>					7		13	4	2	6	4	3	3	1	16	1	3
<i>Caseolus abjectus</i> agg.	1	28															

(continues)

FOSSIL LAND SNAILS OF PORTO SANTO

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(continued)

Species/Samples	A/I	0.63	0.59	0.58	0.51	0.46	0.43	n/a	0.42	0.35	0.33	0.13	0.13	0.05	0.03	n/a	0.02
		15	16	7	6	1	12	17	14	13	11	18	10	3	5	9	4
<i>Caseolus subcalliferus submajor</i>			7	2	90	7	7	11	8	2		1	9	3	3	10	
<i>Caseolus subcalliferus subcalliferus</i>											2					1	
<i>Caseolus hartungi</i>																	
<i>Caseolus punctulatus</i>		12	7	10	55	35	25	17	8	3	2	2	14	3	15	8	21
<i>Caseolus bowdichianus</i>		5	3	8		25	2	20	17	5	1	7	9	3	6	10	5
<i>Actinella arcinella pap.</i>		2	4		1			4	4		1		8	1		2	1
<i>Actinella crassiuscula</i>																	
<i>Actinella effugiens</i>		6	9			15	2		4	4	2		1	5	10	3	2
<i>Discula rotula</i>									3	5	3		2			12	
<i>Discula bicarinata</i>																1	
<i>Discula bicarinata aucta</i>		3	20														
<i>Discula oxytropis</i>						17	11		10	5							
<i>Discula cheiranticola</i>				1	25		12			5							
<i>Discula calcigena</i>																	
<i>Discula pulvinata</i>		3	2			14		15			1						
<i>Discula attrita</i>																	
<i>Discula bulweri</i>																	
<i>Discula cockerelli</i>																	
<i>Discula tectiformis</i>		10	9	4	4	10	2	12	4	3	4	3	9	6	2	7	3
<i>Pseudocampylaea portosantana</i>		15	8			7	3	1	4	4					5		12
<i>Pseudocampylaea lowei</i>											14	7				2	
<i>Leptaxis sp.</i>																	
<i>Leptaxis chrysomela</i>																	
<i>Leptaxis cf. fluctuosa</i>					2	3	2		2	1			1			5	
<i>Leptaxis nivosa</i>		6	6	6		43	17	7	22	15	7	2	27	4	3	13	4
<i>Leptaxis wollastoni</i>		2	8	3		7	3	1	19	7					1		
<i>Lampadia webbiana</i>																	
<i>Helix subplicata</i>		2								3							
<i>Theba pisana</i>																	
No. of taxa	21	22	279	15	7	21	20	17	22	23	19	14	18	13	15	21	13
No. of shells	147	279	279	59	189	259	159	201	202	117	137	172	176	40	115	199	73

APPENDIX 6

Taxa recorded at Site 12, and at Site 10 (included in the sequence), samples arranged by A/I ratios.

A/I	0.512	0.504	0.442	0.431	0.395	0.329
Species/Samples	12-4	12-3	10	12-2	12-1	12-5
<i>Craspedopoma mucronatum</i>						
<i>Truncatellina linearis</i>						1
<i>Staurodon saxicola</i>					1	
<i>Leiostyla subcorneocostata</i>						
<i>Leiostyla calathiscus</i>						7
<i>Leiostyla monticola</i>					2	2
<i>Phenacolimax portosanctanus</i>						
<i>Amphorella melampoides</i>	15	8	6		15	
<i>Amphorella triticea</i>				14	28	15
<i>Amphorella oryza</i>	4	5				7
<i>Amphorella gracilis</i>						
<i>Cylichnidia ovuliformis</i>						3
<i>Boettgeria lowei</i>			2		6	1
<i>Heterostoma paupercula</i>		6	2	3		13
<i>Geomitra coronata</i>	10	12	4	31	50	4
<i>Spirorbula obtecta</i>	4	7	2	2	1	4
<i>Spirorbula depauperata</i>	13	23	10	14	25	14
<i>Caseolus compactus</i> (large)						
<i>Caseolus compactus</i> (small)						13
<i>Caseolus compactus vigiae</i>				2		
<i>Caseolus consors</i>	2		2	19	54	19
<i>Caseolus abjectus</i> agg.	4	20		6	12	19
<i>Caseolus subcalliferus submajor</i>						
<i>Caseolus subcalliferus subcalliferus</i>					1	1
<i>Caseolus hartungi</i>						
<i>Caseolus punctulatus</i>	15	15	5	4	6	8
<i>Caseolus bowdichianus</i>	9	2				
<i>Actinella arcinella</i> pap.		1		1		
<i>Actinella crassiuscula</i>						
<i>Actinella effugiens</i>	43	12		8	5	13
<i>Discula rotula</i>						
<i>Discula bicarinata</i>						
<i>Discula bicarinata aucta</i>						
<i>Discula oxytropis</i>	5	21	4	10	34	5
<i>Discula cheiranticola</i>						
<i>Discula calcigena</i>	4		3			7
<i>Discula pulvinata</i>						
<i>Discula attrita</i>						
<i>Discula bulwerii</i>		5		4	6	2
<i>Discula cockerelli</i>	7					
<i>Discula tectiformis</i>		1			3	
<i>Pseudocampylaea portosanctana</i>	12	9	7		2	2
<i>Pseudocampylaea lowei</i>				4	1	2
<i>Leptaxis</i> sp.						
<i>Leptaxis chrysomela</i>						
<i>Leptaxis</i> cf. <i>fluctuosa</i>						1

(continues)

(continued)

A/I Species/Samples	0.512 12-4	0.504 12-3	0.442 10	0.431 12-2	0.395 12-1	0.329 12-5
<i>Leptaxis nivosa</i>	20	12	5	1		
<i>Leptaxis wollastoni</i>	13	2	1			1
<i>Lampadia webbiana</i>						
<i>Helix subplicata</i>	5	2		5	3	
<i>Theba pisana</i>						
No. of taxa	17	18	13	16	19	24
No. of shells	185	163	53	128	255	164

APPENDIX 7

Taxa recorded by MBS at Fonte da Areia, site S3 (equivalent to Site 1 in the GAG series). Sites are arranged in stratigraphical sequence; no A/I determinations are available. Numbering follows original MBS field notes. *C. abjectus** = Identified as *C. commixtus*; *L. fluctuosa*** = rather *L. erubescens*-like. All "small" *C. compactus* were *C. c. ariensis*. This is not true for other sequences, and the distinction made between large and small elsewhere may not apply here. See Fig. 3 for the alignment of this series with Site 1. Note that *Caseolus calculus*, recorded only here, is not listed in any other appendix.

Stratigraphical sequence	oldest										youngest
Species/Samples	27	26.35	26.21	26.9	26.1	28.2	28.1	29.1	30.1	29.17	25.1
<i>Craspedopoma mucronatum</i>						5			2		
<i>Truncatellina linearis</i>	8						14				
<i>Staurodon saxicola</i>							2				
<i>Leiostyla subcorneocostata</i>								1			
<i>Leiostyla calathiscus</i>	1					3		1	3		
<i>Leiostyla monticola</i>							3				
<i>Phenacolimax portosanctanus</i>								2			
<i>Amphorella melampoides</i>											
<i>Amphorella triticea</i>	2					6	4		8	12	7
<i>Amphorella oryza</i>						1	1				
<i>Amphorella gracilis</i>											
<i>Cylichnidia ovuliformis</i>											
<i>Boettgeria lowei</i>											
<i>Heterostoma paupercula</i>	74	6	5	2		7	8		4	6	69
<i>Geomitra coronata</i>	56	6	5	2		4	11	1	23	22	9
<i>Spirorbula oblecta</i>	10	3	1				1		10	5	
<i>Spirorbula depauperata</i>	50	7	5	4		9	26		6	25	7
<i>Caseolus compactus</i> (large)	266	78	41	29	25	49	83	3	67	26	49
<i>Caseolus compactus</i> (small)								50		50	47
<i>Caseolus cf. compactus vigiae</i>		1	16	10			14	10	1	18	25
<i>Caseolus consors</i>											
<i>Caseolus abjectus</i> agg.	36					6*	10		46	7	
<i>Caseolus subcalliferus submajor</i>		11			1		10	15		13	2
<i>Caseolus s. subcalliferus</i>			3								
<i>Caseolus hartungi</i>											
<i>Caseolus calculus</i>			10	2	4					2	

(continues)

(continued)

Stratigraphical sequence	oldest											youngest
Species/Samples	27	26.35	26.21	26.9	26.1	28.2	28.1	29.1	30.1	29.17	25.1	
<i>Caseolus punctulatus</i>				2		6	1	26	3	4		
<i>Caseolus bowdichianus</i>		9	1		3	1	5	19		2	2	
<i>Actinella arcinella</i> pap.	9								8	7		
<i>Actinella crassiuscula</i>												
<i>Actinella effugiens</i>												
<i>Discula rotula</i>												
<i>Discula bicarinata</i>												
<i>Discula bicarinata aucta</i>									3			
<i>Discula oxytropis</i>												
<i>Discula cheiranticola</i>												
<i>Discula calcigena</i>								2				
<i>Discula pulvinata</i>											1	
<i>Discula attrita</i>			1	1	15				3	2		
<i>Discula bulwerii</i>												
<i>Discula cockerelli</i>												
<i>Discula tectiformis</i>	1				6		2	45		2	12	
<i>Pseudocampylaea</i>												
<i>portosantana</i>												
<i>Pseudocampylaea lowei</i>												
<i>Leptaxis</i> sp.												
<i>Leptaxis chrysomela</i>	1					1	1	19		5	3	
<i>Leptaxis</i> cf. <i>fluctuosa</i>									1**			
<i>Leptaxis nivosa</i>	2	3	2	1	1	2	5	3	2	7		
<i>Leptaxis wollastoni</i>												
<i>Lampadia webbiana</i>												
<i>Helix subplicata</i>	5						1					
<i>Theba pisana</i>												
No. of taxa	14	9	11	9	7	13	19	14	16	18	12	
No. of shells	525	124	90	53	55	100	202	197	190	215	233	

APPENDIX 8

Taxa in samples made by MBS at Sites S2 and S1, samples arranged in ascending stratigraphical position in each site. No A/I data are available. Numbers in bold refer to species unique to Site S2, and which are not listed in any other appendix.

Species/Samples	Porto da Morena S2			Ponta da Canaveira S1			
	3	2	1	4	3	2	1
<i>Craspedopoma mucronatum</i>	1		52				
<i>Truncatellina linearis</i>		21	185	26			
<i>Staurodina saxicola</i>			7				
<i>Leiostyla subcorneocostata</i>		3	30	2			
<i>Leiostyla espigaoensis</i>		4	152				
<i>Leiostyla calathiscus</i>							
<i>Leiostyla monticola</i>							
<i>Punctum pygmaeum</i>		1	42				

(continues)

(continued)

Species/Samples	Porto da Morena S2			Ponta da Canaveira S1			
	3	2	1	4	3	2	1
<i>Playgyrona placida</i>		2	1				
<i>Phenacolimax crassus</i>	1						
<i>Phenacolimax portosanctanus</i>			4				
<i>Amphorella melampoides</i>			1				
<i>Amphorella triticea</i>	3	5	181			2	
<i>Amphorella oryza</i>							
<i>Amphorella gracilis</i>							
<i>Amphorella cf. cimensis</i>			2				
<i>Cylichnidia ovuliformis</i>							
<i>Boettgeria lowei</i>				4			
<i>Heterostoma paupercula</i>	2	4	121	44	6	9	36
<i>Geomitra coronata</i>		1	113	22		3	1
<i>Geomitra acarinata</i>		3	106				
<i>Spirorbula oblecta</i>	1		12	3	6	1	
<i>Spirorbula depauperata</i>	5	6	96	9		3	1
<i>Caseolus compactus</i> (large)							9
<i>Caseolus compactus</i> (small)	11	2	173	45	10	10	19
<i>Caseolus cf. compactus vigiae</i>							
<i>Caseolus consors</i>				2			31
<i>Caseolus abjectus</i> agg.	2	1	82	68	1	22	
<i>Caseolus subcalliferus submajor</i>				10	9	2	
<i>Caseolus s. subcalliferus</i>							
<i>Caseolus hartungi</i>			1				
<i>Caseolus punctulatus</i>	2	9	21	27	6	11	25
<i>Caseolus bowdichianus</i>				1			
<i>Actinella arcinella</i> pap.				6			
<i>Actinella crassiuscula</i>							
<i>Actinella effugiens</i>	1		29	11	5	5	
<i>Actinella morenensis</i>		4	130				
<i>Discula rotula</i>							
<i>Discula bicarinata</i>							
<i>Discula bicarinata aucta</i>				11		1	
<i>Discula oxytropis</i>							
<i>Discula cheiranticola</i>							
<i>Discula calcigena</i>	23		5				
<i>Discula pulvinata</i>					3		84
<i>Discula attrita</i>				1		1	
<i>Discula bulwerii</i>							
<i>Discula cockerelli</i>							
<i>Discula tectiformis</i>					27	1	12
<i>Pseudocampylaea portosanctana</i>							
<i>Pseudocampylaea lowei</i>			11				
<i>Leptaxis</i> sp.		20	4				
<i>Leptaxis chrysomela</i>							
<i>Leptaxis cf. fluctuosa</i>	1	11	23			1	3
<i>Leptaxis nivosa</i>	5		6	1	19	1	17
<i>Leptaxis wollastoni</i>							
<i>Helix subplicata</i>				1			
<i>Theba pisana</i>		1					
No. of taxa	13	17	27	19	10	15	11
No. of shells	58	98	1707	294	92	73	238

APPENDIX 9

Taxa in GAG sites with only one or two samples, arranged by A/I ratio or stratigraphy within sites when possible. Site 8: Ilheu do Baixo; Site 3: Ponta da Calheta; Site 11: Ilheu de Ferro; Site 4: São Sebastião; Site 5: Barbara Gomez.

* = including one aberrant, very tall shell, possibly an unrecognised species. Site 4-2 is stratigraphically above 4-1, and 5-1 is above 5-2.

A/I	0.533	0.362	0.517	n/a	n/a	0.639	n/a	0.611	n/a
Species/Sites/Samples	8-1	8-2	3-1	11-1	9-1	4-1	4-2	5-2	5-1
<i>Craspedopoma mucronatum</i>									
<i>Truncatellina linearis</i>									
<i>Staurodon saxicola</i>									
<i>Leiostyla subcorneocostata</i>									
<i>Leiostyla calathiscus</i>									
<i>Leiostyla monticola</i>									
<i>Phenacolimax portosanctanus</i>									
<i>Amphorella melampoides</i>									
<i>Amphorella triticea</i>			1					2	
<i>Amphorella oryza</i>									
<i>Amphorella gracilis</i>									
<i>Cylichnidia ovuliformis</i>									
<i>Boettgeria lowei</i>									
<i>Heterostoma paupercula</i>	9	1	7		27			1	13
<i>Geomitra coronata</i>		4	2					3	
<i>Spirorbula oblecta</i>	3		3	3	2			2	4
<i>Spirorbula depauperata</i>		10	7	15			1	6	2
<i>Caseolus compactus</i> (large)	9	6				4		1	4
<i>Caseolus compactus</i> (small)		36	13			13	6	4	12
<i>Caseolus compactus vigiae</i>									2
<i>Caseolus consors</i>									
<i>Caseolus abjectus</i> agg.	6	6			6			4	
<i>Caseolus subcalliferus submajor</i>		38*	8			4		7	
<i>Caseolus s. subcalliferus</i>									1
<i>Caseolus hartungi</i>	2				5				
<i>Caseolus punctulatus</i>	27	11	12	16	6	62	10	26	4
<i>Caseolus bowdichianus</i>	4	2	14				25	6	10
<i>Actinella arcinella</i> pap.		11	1						1
<i>Actinella crassiuscula</i>									
<i>Actinella effugiens</i>		3		10					
<i>Discula rotula</i>									
<i>Discula bicarinata</i>									
<i>Discula bicarinata aucta</i>									
<i>Discula oxytropis</i>									
<i>Discula cheiranticola</i>		13							
<i>Discula calcigena</i>		7		11	8				1
<i>Discula pulvinata</i>							10		1
<i>Discula attrita</i>	6	4	1			4			
<i>Discula bulwerii</i>									
<i>Discula cockerelli</i>									
<i>Discula tectiformis</i>		3	8			3	25	3	1

(continues)

(continued)

A/I Species/Sites/Samples	0.533 8-1	0.362 8-2	0.517 3-1	n/a 11-1	n/a 9-1	0.639 4-1	n/a 4-2	0.611 5-2	n/a 5-1
<i>Pseudocampylaea portosantana</i>					3				
<i>Pseudocampylaea lowei</i>					4				
<i>Leptaxis</i> sp.						3			
<i>Leptaxis chrysomela</i>									
<i>Leptaxis</i> cf. <i>fluctuosa</i>		12				3	14	6	2
<i>Leptaxis nivosa</i>		9	7	12			5	25	4
<i>Leptaxis wollastoni</i>									
<i>Lampadia webbiana</i>									
<i>Helix subplicata</i>			8						1
<i>Theba pisana</i>					21				44
No. of taxa	8	17	14	6	9	8	8	14	17
No. of shells	66	176	92	67	82	96	96	96	107

